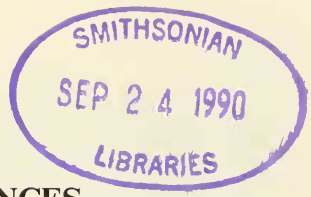


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PROCEEDINGS  
OF THE  
CALIFORNIA ACADEMY OF SCIENCES

Vol. 46, No. 14, pp. 299-326, 12 figs.

September 11, 1990

NEW SPECIES AND NEW COMBINATIONS IN *BLAKEA* AND  
*TOPOBEA* (MELASTOMATACEAE), WITH AN HISTORICAL  
PERSPECTIVE ON GENERIC LIMITS IN  
THE TRIBE BLAKEEAE

By

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ABSTRACT: *Blakea* P. Browne and *Topobea* Aublet, the two currently recognized genera in the Blakeeae have been variously combined and segregated during their long history. A synoptic taxonomic history of these genera is presented with special attention given to characters used to combine or separate them. In keeping with traditional generic concepts, *Blakea* and *Topobea* are maintained and a revised generic key is provided to accommodate anomalous or unusual Mesoamerican species. Descriptions, diagnostic illustrations, discussions, and distribution maps are presented for four new species of *Blakea* (*B. gregii*, *B. hammelii*, and *B. herrerae* from Panama; and *B. scarlatina* from Costa Rica and Nicaragua) and three new species of *Topobea* (*T. fragrantissima*, *T. hexandra*, and *T. suaveolens* from Panama). The study of recently collected flowering material of *B. crassifolia* and *B. parvifolia* necessitates their transfer to *Topobea* and the adoption of a new name, *T. caliginosa*, for the narrow Panamanian endemic previously known as *B. micrantha*.

Received February 2, 1990. Accepted March 14, 1990.

INTRODUCTION

The largely pantropical Melastomataceae comprise some 200 genera and approximately 4,800 species. This comparatively large natural family has traditionally been divided into fourteen tribes based on fruit characters, staminal features, and seed morphology. Of the eight tribes restricted to the western hemisphere, only the Blakeeae and Miconieae are berry-fruited. The Blakeeae are readily recognized by their axillary flowers that are individually subtended by two pairs of decussate bracts, ovoid to pyramidal smooth seeds, and wood with multiseriate rays and frequent occurrence of druses (Koek-Noorman et al. 1979; ter Welle and Koek-Noorman 1981).

The striking morphological isolation of the Blakeeae within the family and the homogeneity of its constituent taxa undoubtedly account for the fact that its tribal status has not been seriously challenged since it was established by Bentham and Hooker (1867). However, *Blakea* P. Browne and *Topobea* Aublet, the two currently recognized genera in the tribe, have been variously combined and segregated during their long history.

Recent fieldwork done in connection with the preparation of a treatment of Melastomataceae for Flora Mesoamericana has resulted in the discovery of several undescribed species in the Blakeeae. An effort to devise a rational basis for assigning these taxa to one genus or the other has necessitated another look at generic limits in the

tribe. I recently expressed serious reservations about the continued recognition of *Topobea* and even suggested that it be submerged in the older and larger genus *Blakea* (Almeda 1989). Additional study of this problem, coupled with the paucity of information on pollen morphology (Patel et al. 1985) and chromosome numbers (Solt and Wurdack 1980), has led me to refrain from merging *Blakea* and *Topobea* without a comprehensive study throughout the extensive neotropical range of these genera.

The following summary provides a synoptic taxonomic history of *Blakea* and *Topobea* together with an assessment of the diagnostic features used to combine or separate them. This is followed by descriptions of four new species of *Blakea*, three new species of *Topobea*, and three generic transfers. Working within the constraints of a geographically defined study, my decision to recognize *Blakea* and *Topobea* is, of necessity, tempered by the historical consensus of opinion among specialists in the family and the need for more data. Nevertheless, a slight modification of original generic concepts is necessary to accommodate the accretion of new and unusual Central American species.

#### SYNOPTIC HISTORY OF *BLAKEA* AND *TOPOBEA*

The genus *Blakea* was first defined by Patrick Browne (1756) for a Jamaican species that was subsequently given the binomial *B. trinervia* by Linnaeus (1759). Browne's circumscription of *Blakea* included a plate and a brief diagnosis describing it as a shrub with nitid trinerved elliptic leaves, 6-merous axillary flowers, and triangular laterally connate anthers. The plate is generalized and provides no details of anther morphology. The terse description is sufficient, however, to preclude confusion with the allied genus *Topobea*, which was described and illustrated by Aublet (1775) from material collected in French Guiana. Although many of Aublet's published drawings are mixtures and some of his descriptions are composites of discordant elements (Howard 1983), both the plate and description of *T. parasitica* emphasize the oblong subulate anthers that are typical of so many species in this genus. Curiously, Aublet overlooked or chose not to describe and illustrate the broad, gaping, dorsally inclined, confluent anther pores. This is another diagnostic character that

figures prominently in decisions to maintain *Topobea* as a distinct genus. In choosing the epithet *parasitica*, Aublet was responsible for perpetrating a misunderstanding of the epiphytic habit that is common to so many species of *Blakea* and *Topobea*.

The younger Linnaeus (1781) and de Jussieu (1789) maintained *Blakea* and *Topobea* as defined by Aublet. By retaining *Blakea quinque-nervia* Aublet [= *Bellucia grossularioides* (L.) Triana] in *Blakea*, it is clear that their interpretation was a broad one that included at least two genera now relegated to two different berry-fruited tribes.

David Don (1823), in an early paper devoted to the Melastomataceae, was the first to part ranks with his predecessors by merging *Topobea* and *Blakea*. His decision, however, was based on characters other than anther morphology. The weakness of Don's argument is best conveyed by his own words: "Although the *Topobea* of Aublet recedes somewhat from *Blakea*, in its being parasitical; yet, notwithstanding, in the Lambertian Herbarium are several unpublished species, from Don Jose Pavon, natives of Peru, and not parasitical, which agree with *Topobea* in every essential point; and these also, accord well with *Blakea*, except in having four, instead of six scales, surrounding the calyx, which, however, is a variable character; and, therefore I think myself justified in uniting these two genera." De Candolle (1828) also adopted this interpretation in his *Prodromus*. Like Don and his immediate predecessors, de Candolle's broad generic concept of *Blakea* included species now recognized in *Bellucia*.

Naudin (1852) rejected this inclusive disposition and emphasized diversity in anther morphology and habit as reasons for resurrecting *Topobea*. He provided no involved explanation to justify his decision, yet he described a new genus, *Pyxidanthus*, to accommodate three new species that he considered closely related to *Blakea*. The concept of *Blakea* and *Topobea* espoused by Naudin was faithfully followed by Bentham and Hooker (1867) without comment.

Triana (1871), as astute specialist in the Melastomataceae, synonymized *Pyxidanthus* under *Blakea* along with *Valdesia* Ruiz and Pavon, another minor generic segregate. *Pyxidanthus*, *Valdesia*, and the subsequently described *Amaraboya* Linden are now universally accepted synonyms of *Blakea*. As recognized by Triana (1871),

*Blakea* included those species with short, oval or elliptic, apically blunt or rounded anthers with two minute well-separated pores. *Topobea* included those species with linear-oblong or subulate anthers with two confluent dorsally inclined pores. Baillon (1879), who was noted for his broad view of generic limits, was unimpressed by these differences in anther morphology. He returned *Topobea* to the synonymy of *Blakea* but provided no convincing reasons aside from a comment describing the anthers of *Topobea* as more elongate and narrower than those in *Blakea*. For a botanist who excelled in character analysis, Baillon's brief treatment of these genera reflects a superficial understanding of the anther differences between them.

The most comprehensive and perhaps most influential accounts of generic limits in the Blakeae are those of Cogniaux (1888, 1891). Cogniaux was undoubtedly influenced by Triana. Unlike Triana, however, he was the first to provide the following explicit key clarifying the distinctions between *Blakea* and *Topobea* as he understood them:

- A. Stamina filamenta crassiuscula, antherae breves, obtusae a latere compressae, connectivo crassissimo, postice calcarato ..... *Blakea*
- B. Stamina filamenta filiformia; antherae lineari vel oblongo-subulatae, rostratae, connectivo mediocri, interdum ecalcarato ..... *Topobea*

These differences amply characterized the species then known to Cogniaux, but they cannot be used for a strict characterization of the two genera at present. The short, obtuse, laterally compressed anthers of *Blakea* (Fig. 2A, C, E; Fig. 3A, E) versus the linear to oblong-subulate rostrate anthers of *Topobea* (Fig. 1E, F; 2B; 3B, C) are the only modal contrasts that appear to be valid for distinguishing the majority of species now assigned to these genera. The differences in filament thickness and presence or absence of dorsal appendages on the connective are inconsistent criteria for differentiating *Blakea* and *Topobea*. Like his predecessors, Cogniaux neglected to emphasize that *Blakea* has anthers with two typically minute and well-separated pores and *Topobea* has two (rarely one) broad approximate or confluent dorsally inclined pores. The generic concepts promoted by Cogniaux have been adopted by all subsequent specialists (Almeda,

in press; Gleason 1935, 1958; Wurdack 1973, 1980) and other authors of major regional treatments of the Melastomataceae (Standley 1924, 1938; Standley and Williams 1963), except Macbride (1941). Invoking a rationale similar to that of Baillon, Macbride combined *Blakea* and *Topobea* and commented on the inconsistency of the filament character used as a diagnostic feature by Cogniaux.

In a paper describing many new species of *Blakea* and *Topobea*, Gleason (1945) sympathized with, but rejected, Macbride's view. The close relationship between these two genera is readily apparent in their many parallel and overlapping variations in habit, leaves, indument, floral bracts, petals, calyx lobes, ovary cell number, and seeds. Although Baillon (1879) and Macbride (1941) intimated that anther characters provide insufficient grounds on which to base the recognition of genera, Gleason (1945, 1947), who defended their use, pointed out that specimens can be sorted precisely into one genus or the other when staminal material is available.

According to Patel (in litt., 18 July 1985), preliminary results of a numerical taxonomic analysis of pollen (using SEM data) in the Melastomataceae reveal that *Blakea* and *Topobea* sort out into different clusters. Because pollen of Melastomataceae is diverse exomorphically (Patel et al. 1985), an expanded survey is needed to extend and refine these observations.

Until more information about micromorphological characters such as chromosome numbers, pollen morphology, and chemistry is available, it seems preferable to adhere to traditional generic concepts until we can rest decisions on a broader data base than was available to our predecessors.

This, however, does not ease the current difficulty of assigning the few unusual species to one genus or the other. In the Mesoamerican region, at least four different species groups are problematic in determining where to draw the line between *Blakea* and *Topobea*. I will consider the relationships among *Blakea wilburiana* Almeda and allied species in a future paper. The other three species groups are mentioned here because at least one species from each is newly described below.

The first of these, *Blakea gregii*, belongs to a group of five closely related species characterized by nectar-producing pendant flowers with green petals. The anthers of *B. gregii* are elliptic-oblong

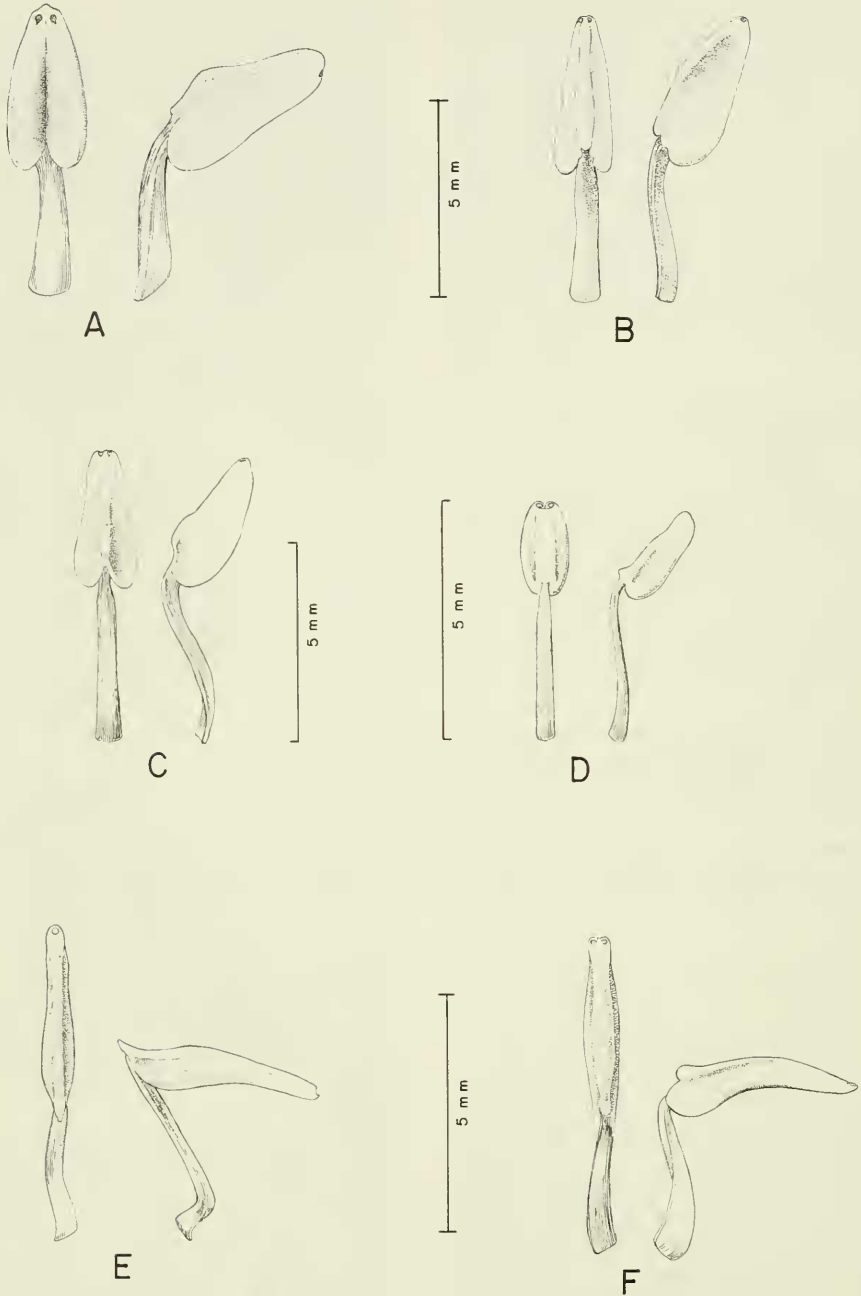


FIGURE 1. Representative stamen morphology in *Blakea* and *Topobea*. A, *B. wilburiana* Almeda; B, *B. austin-smithii* Standley; C, *B. purpusii* Brandege; D, *T. crassifolia* (Almeda) Almeda; E, *T. pittieri* Cogn.; F, *T. brenesii* Standley. (A from Almeda et al. 6525, CAS; B from Almeda et al. 2145, CAS; C from Breedlove & Almeda 47747, CAS; D from de Nevers 5943, CAS; E from Almeda et al. 3161, CAS; F from Wilbur et al. 15809, DUKE.)

and laterally compressed with two dorsally inclined approximate pores (Fig. 4G). Anther conformation is like that of *Blakea* but the dorsal inclination of the apical pores is more like that

encountered in *Topobea*. The pore width, however, is narrower than that typically found in many species of the latter genus. In deciding to place this species in *Blakea*, I was influenced by

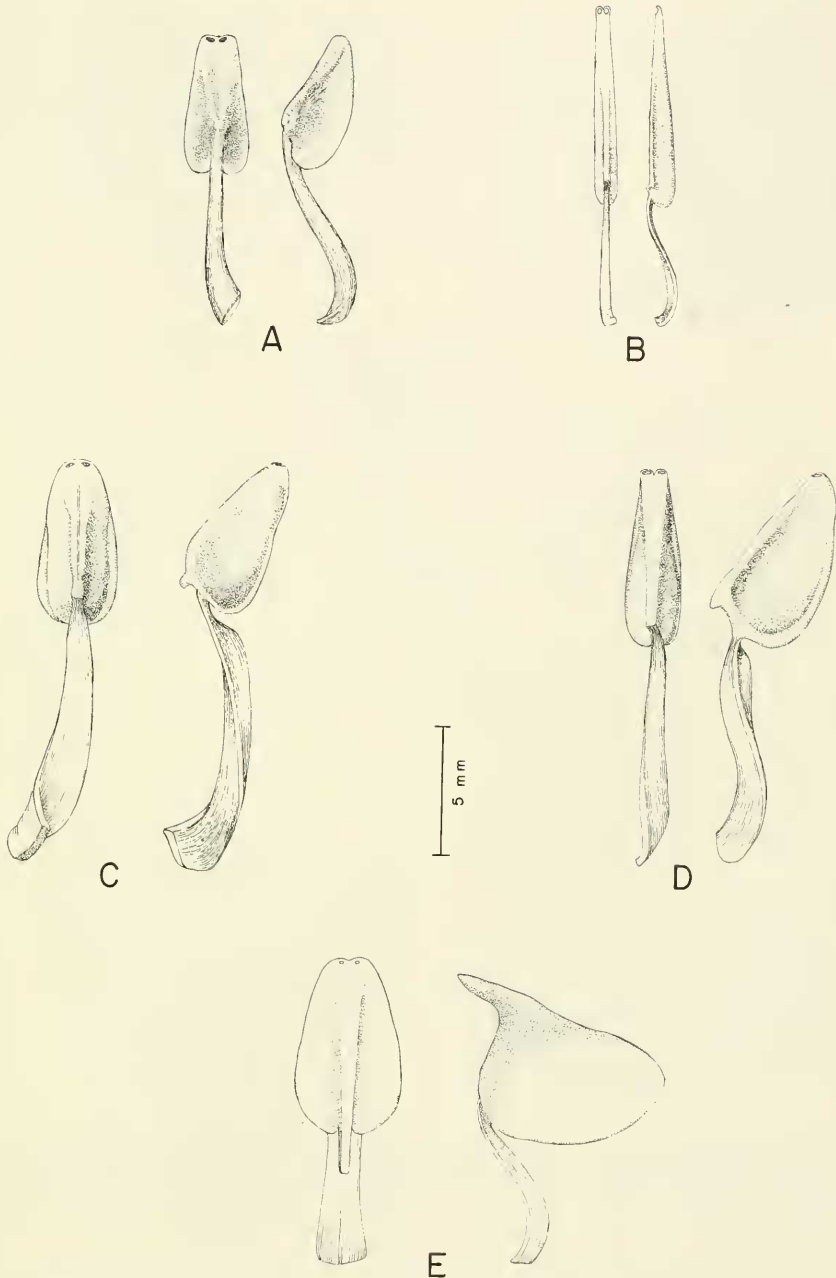


FIGURE 2. Representative stamen morphology in *Blakea* and *Topobea*. A, *B. elliptica* (Gleason) Almeda; B, *T. calycularis* Naudin; C, *B. woodsonii* Gleason; D, *T. storkii* Standley; E, *B. tuberculata* J. D. Smith. (A from Almeda *et al.* 6261, CAS; B from Breedlove 50940, CAS; C from Almeda *et al.* 3046, CAS; D from Almeda *et al.* 2884, CAS; E from Almeda & Nakai 4529, CAS.)

the somewhat more typical *Blakea*-type anthers of its close relatives, *B. austin-smithii* Standley (Fig. 1B) and *B. purpusii* Brandegee (Fig. 1C).

*Topobea hexandra* has been the most difficult

to place generically. It is part of an unusual assemblage in the Blakeeae distinguished by small sessile or short-pedicellate flowers with only six antesealous stamens. Its close relatives include

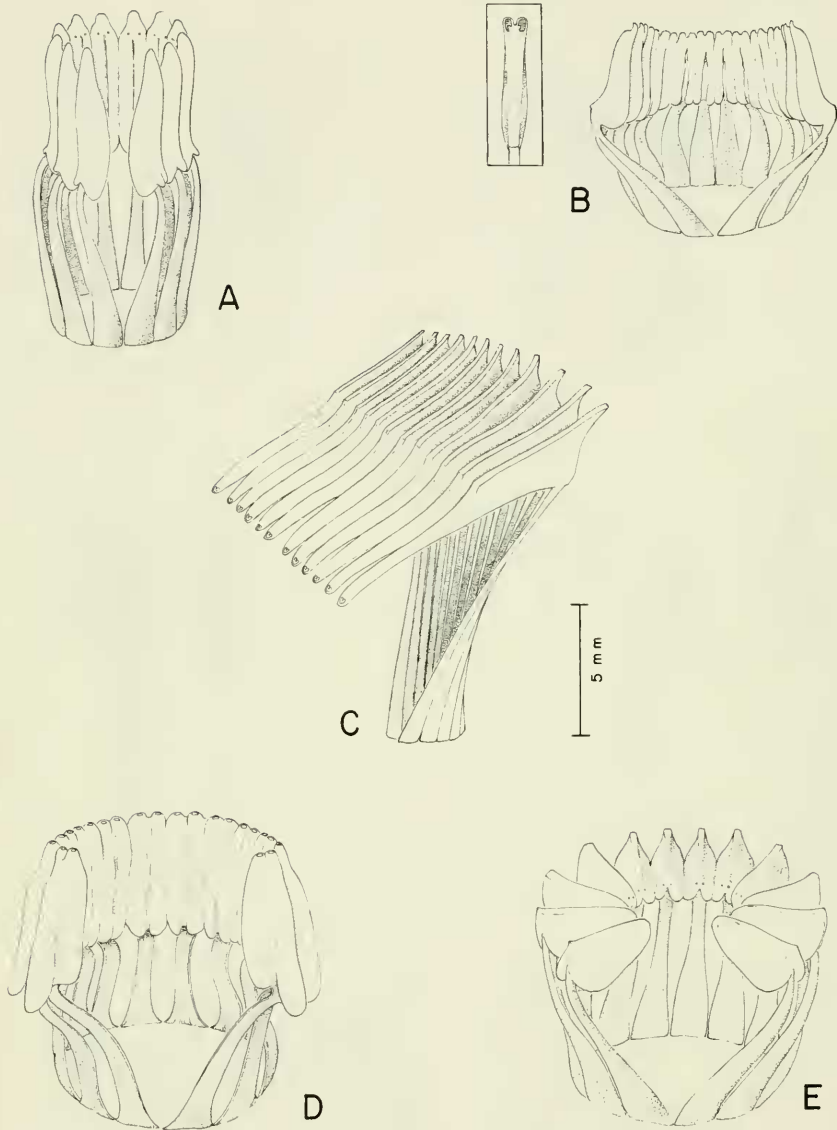


FIGURE 3. Representative stamen morphology in *Blakea* and *Topobea*. A, *B. litoralis* L. O. Williams; B, *T. parvifolia* (Gleason) Almeda; C, *T. albertiae* Wurdack; D, *B. hirsuta* Triana var. *rotundata* Markgraf; E, *B. anomala* J. D. Smith. (A from Almeda & Nakai 4189, CAS; B from Almeda et al. 5898, CAS; C from Almeda et al. 6153, CAS; D from Lugo 4140, CAS; E from Almeda 2655, CAS.)

*T. cordata* Gleason, *T. caliginosa* Almeda, and *T. crassifolia* (Almeda) Almeda. Stamens of *T. cordata* were unknown to Gleason (1950) when he proposed it as a new species. His decision to place it in *Topobea* was based on its superficial resemblance to some sessile-leaved species of that genus. Although each of the species in this complex is known from very few flowering collec-

tions, available anther material exhibits interesting variations on the *Topobea* theme. With the exception of *T. hexandra*, all have anthers with two broad confluent pores. In *T. cordata*, the anthers are oblong-subulate (5–5.5 mm long) and the confluent pores are somewhat ventrally inclined. In *T. caliginosa* and *T. crassifolia* the anthers are linear-oblong but shorter (2–2.5 mm)

with truncate to somewhat dorsally inclined pores (Fig. 1D). The anthers of *T. hexandra* are also short (2 mm) and oblong, but they are laterally compressed and the two apical pores, although broad, are ventrally inclined and separated from one another (Fig. 11F). In the context of variation exhibited by its close relatives, the summation of anther characters in this species argues for placement in *Topobea*. Without these insights, one might be inclined to assign it to *Blakea*.

The last of the problematic species to be considered here is *T. suaveolens* Almeda. This species is unusual in having fragrant pendant flowers with brightly colored petals and connivent anthers that form a ring around the exerted style (Fig. 12C). The essentially elliptic shape and conspicuous lateral compression of the anthers (Fig. 12E) are reminiscent of *Blakea*-type anthers but the broad solitary dorsally inclined apical pore is a feature known only in *Topobea*. Again, my generic placement of this species is influenced by its close relationship to *T. fragrantissima* Almeda (Fig. 10), a species with androecial characters that can only be attributed to *Topobea*.

Interestingly, the anomalous androecial morphology in the cases discussed above all appear to represent derived syndromes. Each is associated with a unique pollen presentation mechanism (*T. suaveolens*), a specialized pollinator spectrum (see discussion under *B. gregii*), or great reduction in flower size (*T. hexandra*). *Blakea*, with about 100 described species, and *Topobea*, with over 60 species, are large and diverse, closely related genera. If more unusual anther forms come to light, it may become increasingly difficult to separate them without establishing arbitrary limits or fueling counterarguments to submerge *Topobea*. For floristic purposes, I find it expedient to recognize both genera. This is done for convenience and to preclude extensive nomenclatural changes pending a comprehensive study of the tribe. It is not done out of a firm conviction that generic status is necessarily the best way to reflect relationships based on currently perceived differences. Accordingly, the following revised key to these genera is offered in an attempt to incorporate the most obvious Mesoamerican anomalies discovered to date:

Stamens 12 in number; anthers 2-pored, oval, oblong, or elliptic, compressed laterally, bluntly obtuse or broadly rounded at the

summit with two typically well-separated (often minute) apical pores ..... *Blakea*  
Stamens 6, 8, or 12 in number; anthers 1-pored or 2-pored, linear-oblong to oblong-subulate or rostrate, usually not compressed laterally (if conspicuously compressed then 1-pored or dorso-basally appendiculate) with approximate or confluent dorsally inclined pores (if pores are prominently inclined ventrally then flowers are hexandrous or pedicels are beset with spreading brown hairs 1–2.5 mm long) ..... *Topobea*

#### NEW TAXA AND NEW COMBINATIONS

##### *Blakea gregii* Almeda, sp. nov.

(Fig. 4)

TYPE:—PANAMA. Chiriquí: Cerro Pate Macho, windswept ridge, 8°49'N, 82°24'W, elev. 2,100 m, 17 Jan. 1986, *de Nevers & McPherson 6840* (holotype: CAS! isotypes: MEXU!, MO!, PMA!, US!).

Frutex ca. 2–4 m altus. Ramuli primum quadrangulati demum teretes sicut petioli laminarum subtus pedicelli bracteaeque pilis 1–2.5 mm longis induti. Petioli 1.8–3.5 cm longi; lamina 9.3–14.5 × 5–9 cm elliptica vel elliptico-ovata apice acuminata basi obtusa vel rotundata vel late acuta, 5-nervata vel 5-plinervata, coriacea et integra, nervis secundariis 3–6 mm inter se distantibus. Flores 6-meri penduli in quoque nodo superiore plerumque 1–4, pedicellis 1.2–2 cm longis; bractea exteriores 7–8 × 5–8 mm ellipticae vel ovato-ellipticae ad basim paulo (2 mm) coalitae; bractea interiores omnino liberae 5–6 × 4–7 mm ovatae vel suborbiculares apice truncato-rotundato. Hypanthium (ad torum) 6 mm longum extus glabrum vel sparse subamorpho-furfuraceum; calycis tubus 2–3 mm longus, lobis 2–4 mm longis extus sparsiuscule strigosis. Petala 13–14 × 9–11 mm obovata apice rotundato sparse caduceque glanduloso-ciliolata. Filamenta 6–7 mm longa; antherae 4–4.5 × 2 cm subulatae lateraliter non cohaerentes, dorsaliter biporosae; connectivum dorsaliter ca. 0.5 mm supra thecarum basim inconspicue tuberculatum. Stylus 1.2–1.3 cm; ovarium 6-loculare et ½ inferum apice glabro (cono et collo non evoluto).

Terrestrial shrubs 2–4 m tall. Young internodes quadrate, becoming rounded with age. Distal branchlets, vegetative buds, petioles, and pedicels densely covered with a brown indument of appressed, ± curved subulate hairs mostly 1–2.5 mm long. Mature leaves of a pair essentially equal in size; petioles 1.8–3.5 cm long; blades coriaceous, 9.3–14.5 cm long and 5–9 cm wide, elliptic to elliptic-ovate, apex acuminate, base obtuse to rounded but sometimes varying to broadly acute, margin entire and somewhat revolute when dry, 5-nerved or 5-plinerved, the innermost pair of primaries diverging from the median nerve 4–6 mm above the blade base, the

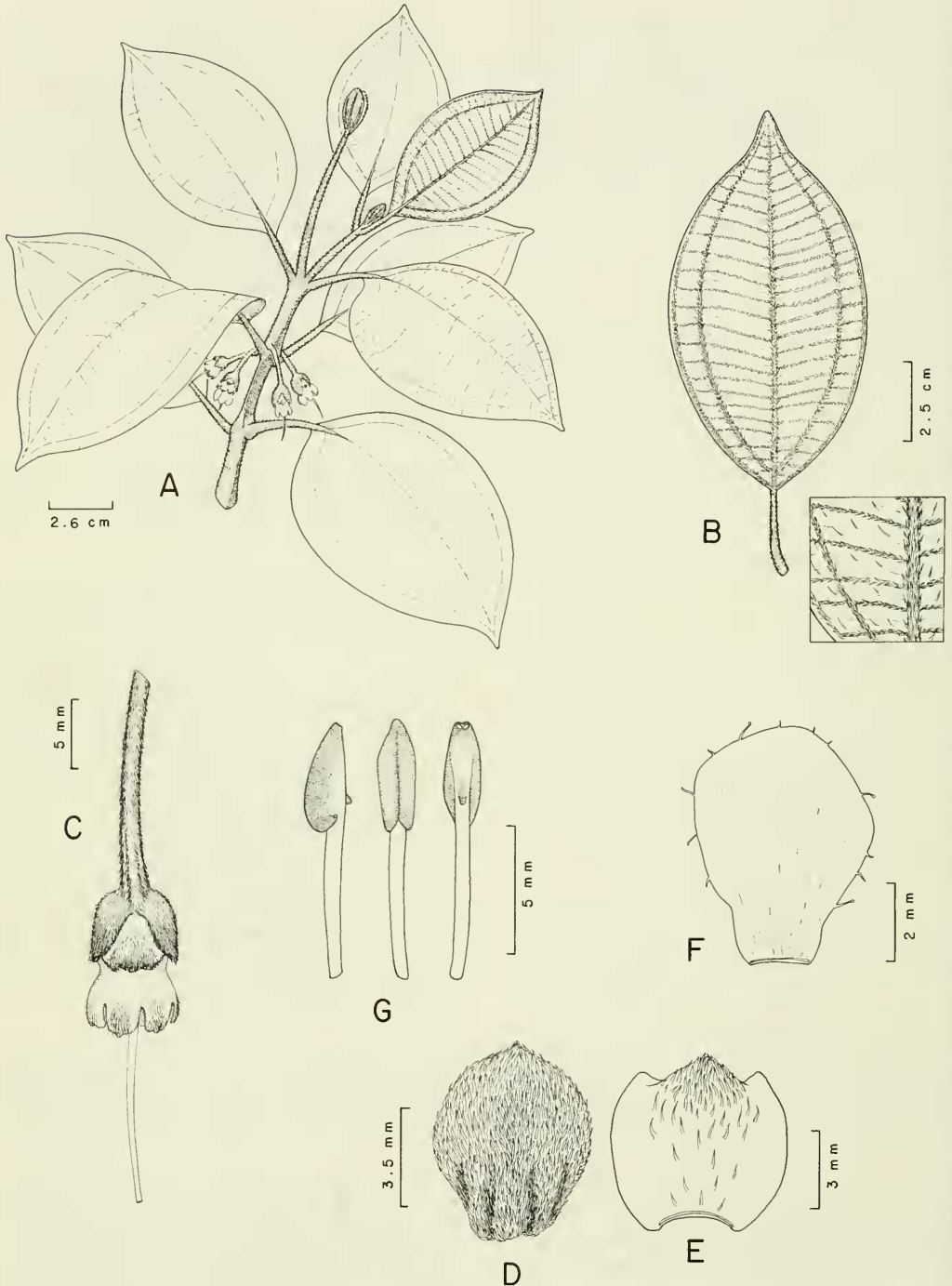


FIGURE 4. *Blakea gregii* Almeda. A, habit; B, representative leaf with enlargement (abaxial surface); C, representative flower (natural posture) with petals and stamens removed; D, outer floral bract (abaxial surface); E, inner floral bract (abaxial surface); F, petals (adaxial surface); G, stamens, lateral view (left), ventral view (middle), dorsal view (right). (A from Almeda *et al.* 6137, CAS; B-G from the holotype.)



elevated network of transverse secondaries spaced 3–6 mm apart at the widest portion of the blade, the young unexpanded leaves beset with a deciduous indument of white woolly hairs but typically becoming glabrous adaxially at maturity and moderately to copiously covered abaxially with smooth appressed to  $\pm$  curved brown hairs 1.5–2.5 mm long. Flowers pendant, solitary, paired, or in fascicles of 4 in the leaf axils of distal branches; pedicels 1.2–2 cm long. Floral bracts thick and semisucculent, sessile and entire; outer bracts connate basally for 2 mm, 7–8  $\times$  5–8 mm, elliptic to elliptic-ovate, apex acute, densely covered abaxially with appressed to incurved smooth brown hairs; inner bracts free to the base, 5–6  $\times$  4–7 mm, ovate to subrotund, apex rounded to truncate varying to retuse with a bluntly acute median lobe, sparingly to moderately beset with appressed brown hairs that are typically concentrated around or restricted to the median apex. Hypanthia (at anthesis) campanulate to suburceolate, 6 mm long to the torus and 7–8 mm in diameter, glabrous or sparingly brown furfuraceous toward the base. Calyx tube 2–3 mm long; calyx lobes erect, 2–4 mm long and 4–5 mm wide basally, ovate to deltoid-ovate with a blunt callose-thickened tooth at the abaxial apex of each lobe, roughened along interlobe sinuses, adaxially glabrous, abaxially covered with a sparse indument of tardily deciduous short incurved brown hairs that are restricted to or largely concentrated near the apex. Petals 6, glabrous, connivent to somewhat imbricate when fully expanded, 13–14  $\times$  9–11 mm, green, obovate, apically rounded, entire but irregularly glandular-ciliate. Stamens 12, isomorphic, free and encircling the exerted style; filaments complanate and glabrous, 6–7 mm long; anthers 4–4.5 mm long, 2 mm wide, elliptic-oblong, laterally compressed, each anther tipped with two dorsally inclined approximate pores; connective dilated dorso-basally ca. 0.5 mm above the filament insertion into a blunt callose spur. Ovary  $\frac{1}{2}$  inferior, 6-celled, glabrous and lobulate at the apex but not expanded into a cone or collar. Style straight, glabrous, 1.2–1.3 cm long, conspicuously exerted beyond the petals and calyx lobes; stigma truncate. Berry globose, about 6 mm long and 8 mm in diameter. Seeds clavate to narrowly pyriform, ca. 1 mm long, beige with a smooth glossy testa and a conspicuous lateral raphe.

**PHENOLOGY.**—Flowering specimens have been

collected in January; the only fruiting specimen was collected in March.

**DISTRIBUTION.**—A little-collected cloud forest or elfin forest species known only from Chiriquí Province, Panama in the region extending from Cerro Horqueta to Cerro Pate Macho at 1,800–2,200 m (Fig. 5).

**ADDITIONAL SPECIMENS EXAMINED.**—PANAMA. Chiriquí: S slopes of Cerro Horqueta, 21 Jan. 1971, *Wilbur et al.* 13486 (CAS, DUKE, MO); Cerro Pate Macho, 8°49'N, 82°24'W, 13 Mar. 1988, *Almeda et al.* 6137 (CAS, CR, MO, NY, PMA, TEX).

*Blakea gregii* is closely related to four other species characterized by cryptic, pendant flowers with green, connivent petals and nocturnal or crepuscular nectar production (Almeda 1980, 1981a). The green-flowered species are typically cloud forest hemiepiphytes that germinate terrestrially, ascend nearby trees by adventitious roots, and ultimately become epiphytic by losing root contact with the soil. Both *B. chlorantha* and *B. gregii*, however, are often conspicuous terrestrial shrubs on windswept ridges of the continental divide where the vegetation is commonly reduced to elfin woodland.

Intensive field studies by Lumer (1981) and Lumer and Schoer (1986) have shown that *B. austin-smithii*, *B. chlorantha*, and *B. penduliflora* are visited and pollinated by six species of rodents belonging to four genera: *Oryzomys*, *Peromyscus*, *Reithrodontomys*, and *Scotinomys*. Lumer and Schoer (1986) suggest that rodents may indeed play a significant role as pollinators of flowering plants in the harsh windy cloud forest environment. Nothing is known about the pollination of *B. gregii*, but similarities in floral morphology and habitat suggest that small rodents may also play an important role in the reproductive biology of this species.

To facilitate comparison, diagnostic characters of the five species of *Blakea* with pendant green flowers are summarized in the following key:

1. Leaf blades modified adaxially at the petiole-laminar junction into flap-like saccate pouches, the basal and lateral margins of which are free from but conspicuously decurrent on the petiole.
2. Pubescence of uppermost internodes consisting of hairs 1–2 mm long; leaf blades bluntly denticulate and revolute on drying; outer floral bracts linear-lan-

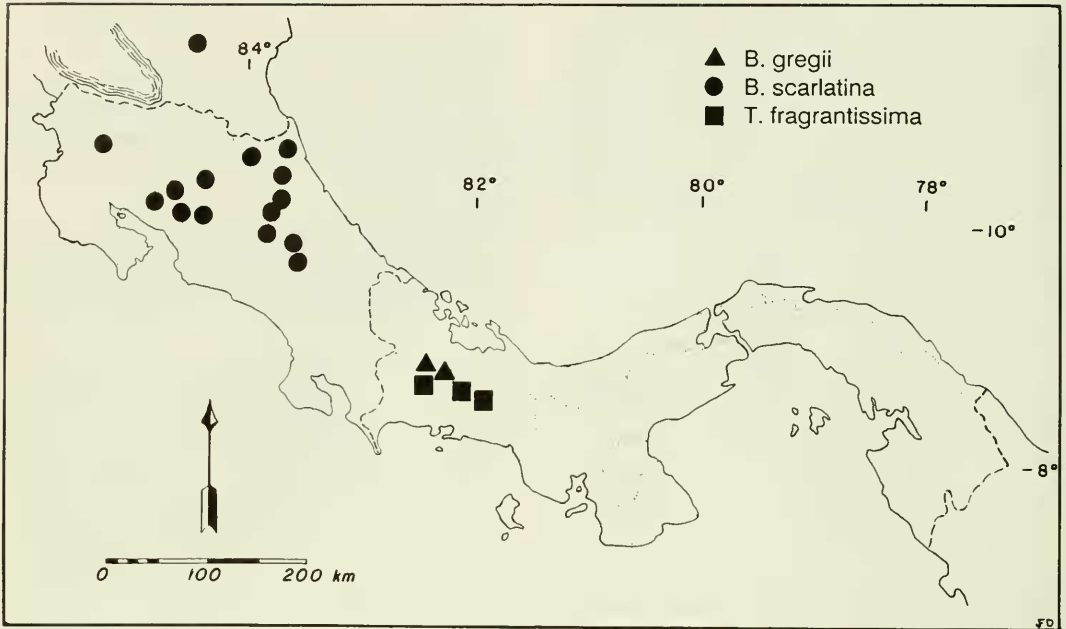


FIGURE 5. Distributions of *Blakea gregii*, *B. scarlatina*, and *Topobea fragrantissima*.

ceolate, 15–21 mm long, equaling or exceeding the calyx lobes at anthesis; Costa Rica (Cerro Chompipe, Volcán Barva, and Volcán Irazú)

..... *B. austin-smithii* Standley

2. Pubescence of uppermost internodes consisting of hairs mostly less than 0.5 mm long; leaf blades entire and revolute on drying; outer floral bracts ovate to elliptic-ovate, 5.5–9 mm long, conspicuously shorter than the calyx lobes at anthesis; Costa Rica (Cordillera de Tilaran) ..... *B. chlorantha* Almeda

1. Leaf blades not modified adaxially at the petiole-laminar junction into flap-like saccate pouches.

3. Older petioles, pedicels, and floral bracts essentially glabrous; outer floral bracts 13–17 mm wide on fruiting hypanthia; Costa Rica (Cordillera de Talamanca and Volcán Barva) .....

..... *B. penduliflora* Almeda

3. Older petioles, pedicels, and floral bracts moderately to copiously covered with appressed or spreading brown hairs; outer floral bracts 5–9 mm wide on fruiting hypanthia.

4. Uppermost internodes and elevated

primary nerves on lower leaf surfaces moderately to densely covered with spreading brown hairs mostly less than 0.5 mm long; pedicels (20–) 28–38 mm long; outer floral bracts 13–20 mm long; Mexico (Chiapas) and western Guatemala (Quezaltenango and San Marcos) .....

..... *B. purpusii* Brandegee

4. Uppermost internodes and elevated primary nerves on lower leaf surfaces densely covered with appressed brown hairs 1–2.5 mm long; pedicels 12–20 mm long; outer floral bracts 7–8 mm long; western Panama (Chiriquí) ..... *B. gregii* Almeda

Among the green-flowered species, *B. gregii* is probably most closely related to *B. chlorantha*. They are separable even in sterile condition because *B. gregii* lacks the flap-like saccate pouches at the petiole-laminar junction that are typical of *B. chlorantha*. The latter also differs consistently in a number of other characters. Pubescence of the upper cauline internodes consists of ± flattened subulate hairs mostly less than 0.5 mm long and the floral bracts are beset with a mixture of spreading shaggy hairs (these mostly

less than 0.5 mm long) and appressed stellate hairs. In addition, the pedicels of *B. chlorantha* are shorter (0.4–1 cm), the calyx lobes are triangular instead of bluntly rounded, and the petals are about half the size (6–8.5 × 5–6 mm) of those in *B. gregii*.

This species is named for Greg de Nevers (1955–), a student of Arecaceae, who collected the type and many other important additions to the melastome flora of Mesoamerica in the course of his extended field work in Panama from 1984 to 1986.

***Blakea hammelii* Almeda, sp. nov.**

(Fig. 6)

TYPE.—PANAMA. Chiriquí: 3.5 mi. NE of Boquete, end of rd. on slope S of Río Palo Alto, 17 Nov. 1978, *Hammel 5688* (holotype: CAS!; isotype: MO).

Frutex epiphyticus vel terrestris. Petioli 0.7–1.7 cm longi; lamina 3.5–7.5 × 1.6–4.5 cm elliptica vel elliptico-ovata apice caudata vel cuspidata basi acuta ad maturitatem subcoriacea et glabra, 5-nervata, nervi in axillis acarodomatii instructi, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli vel bini, pedicellis 2.6–3.5 cm longis, bractee omnino liberae; bractee exteriores 3.5–5 × 2–3 mm ovatae vel ovato-ellipticae extus sparse subamorpho-furfuraceae demum glabratae; bractee interiores 3–4 × 3–3.5 mm oblongo-ovatae extus sparse inconspicueque fimbriolato-ciliolatae. Hypanthium (ad torum) 3–4 mm longum extus glabrum; calycis tubus 1–1.5 mm longus, lobis 1–1.5 × 2.5–3.5 mm. Petala glabra 1.4–1.5 × 0.8–0.9 cm obovata apice rotundato. Filamenta 4.5–5.5 mm longa; antherae 3.5–4 × 1–1.5 mm oblongae lateraliter non cohaerentes apicaliter biporosae; connectivum dorsaliter ca. 1–1.5 mm supra thecarum basim tuberculatum. Stylus 10–11 mm; ovarium 5–6-loculare et  $\frac{2}{3}$  inferum, cono glabro (collo non evoluto).

Epiphytic or terrestrial shrubs or small trees 2.5–6 m tall. Young vegetative buds deciduously furfuraceous, otherwise glabrous, the distal branchlets glabrous and bluntly quadrate with thickened interpetiolar lines or ridges. Mature leaves of a pair equal to unequal in size, glabrous throughout; petioles 0.7–1.7 cm long; blades subcoriaceous, 3.5–7.5 cm long and 1.6–4.5 cm wide, elliptic to elliptic-ovate, apex caudate to cuspidate, base acute, margin entire, 5-nerved abaxially with well-developed, irregularly ruptured domatia formed in the angles between the median vein and each of the two proximal lateral veins, the striolate transverse secondary veins spaced mostly less than 0.25 mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of distal branches; pedicels 2.6–3.5 cm long, glabrous. Floral bracts

sessile, entire, and free to the base; outer bracts 3.5–5 × 2–3 mm, ovate to ovate-lanceolate or elliptic-ovate, apex bluntly acute to rounded, sparingly and deciduously brown furfuraceous-puberulent; inner bracts 3–4 × 3–3.5 mm, oblong-ovate, apex rounded, essentially glabrous but deciduously fimbriolate-puberulent on the margins. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus and 6–7 mm in diameter, glabrous. Calyx tube 1–1.5 mm long; calyx lobes 1–1.5 mm long and 2.5–3.5 mm wide basally, broadly ovate with a blunt callose-thickened tooth at the abaxial apex of each lobe, margin entire, glabrous on both surfaces. Petals 6, glabrous, 1.4–1.5 × 0.8–0.9 cm, white flushed with pink unilaterally on the abaxial surface, obovate, apically rounded, entire. Stamens 12, isomorphic, free and declined to one side of the flower opposing the style; filaments complanate and glabrous, 4.5–5.5 mm long; anthers 3.5–4 mm long, 1–1.5 mm wide, yellow, linear-oblong in dorsal and ventral view, narrowly ovoid in profile view, truncate at the apex with two somewhat dorsally inclined pores; connective slightly thickened dorsally and dilated into a blunt spur ca. 1–1.5 mm above the filament insertion. Ovary  $\frac{2}{3}$  inferior, 5–6-celled, glabrous at the summit which is distended into a prominent cone that becomes rounded with age. Style declinate and somewhat sigmoid, glabrous, 10–11 mm long; stigma truncate. Berry globose, 5–6.5 mm long and 4–7 mm in diameter. Seeds irregularly pyriform to pyramidate, 0.5–1 mm long, beige with a smooth testa and conspicuous lateral raphe.

PHENOLOGY.—Flowering specimens have been collected from January through April and in November; the only known fruiting specimens were collected in January and April.

DISTRIBUTION.—Local and uncommon in cloud forests on the slopes of Cerro Pate Macho and along the Río Palo Alto in Chiriquí Province, Panama at 1,600–1,900 m (Fig. 8).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Chiriquí: S slopes of Cerro Pate Macho, along trail E of Jaramillo Arriba, 8°49'N, 82°23'W, 12 Apr. 1984, *Churchill & Kujit 5103* (CAS); trail to Cerro Pate Macho, 8°49'N, 82°24'W, 17 Jan. 1986, *de Nevers & McPherson 6830* (CAS); back side of mountain, Boquete, 20 Mar. 1977, *Folsom 2185* (CAS); along trail between N fork of Río Palo Alto and Cerro Pate Macho, ca. 6 km NE of Boquete, 8°48'N, 82°23.5'W, 6 Feb. 1986, *Grayum et al. 6371* (CAS); road along Río Palo Alto ca. 3 km NE of Boquete to the end, 15 Apr. 1982, *Huñi 1855* (CAS); Río Palo Alto, 28 Apr. 1983, *Schmalzel 1478* (CAS).

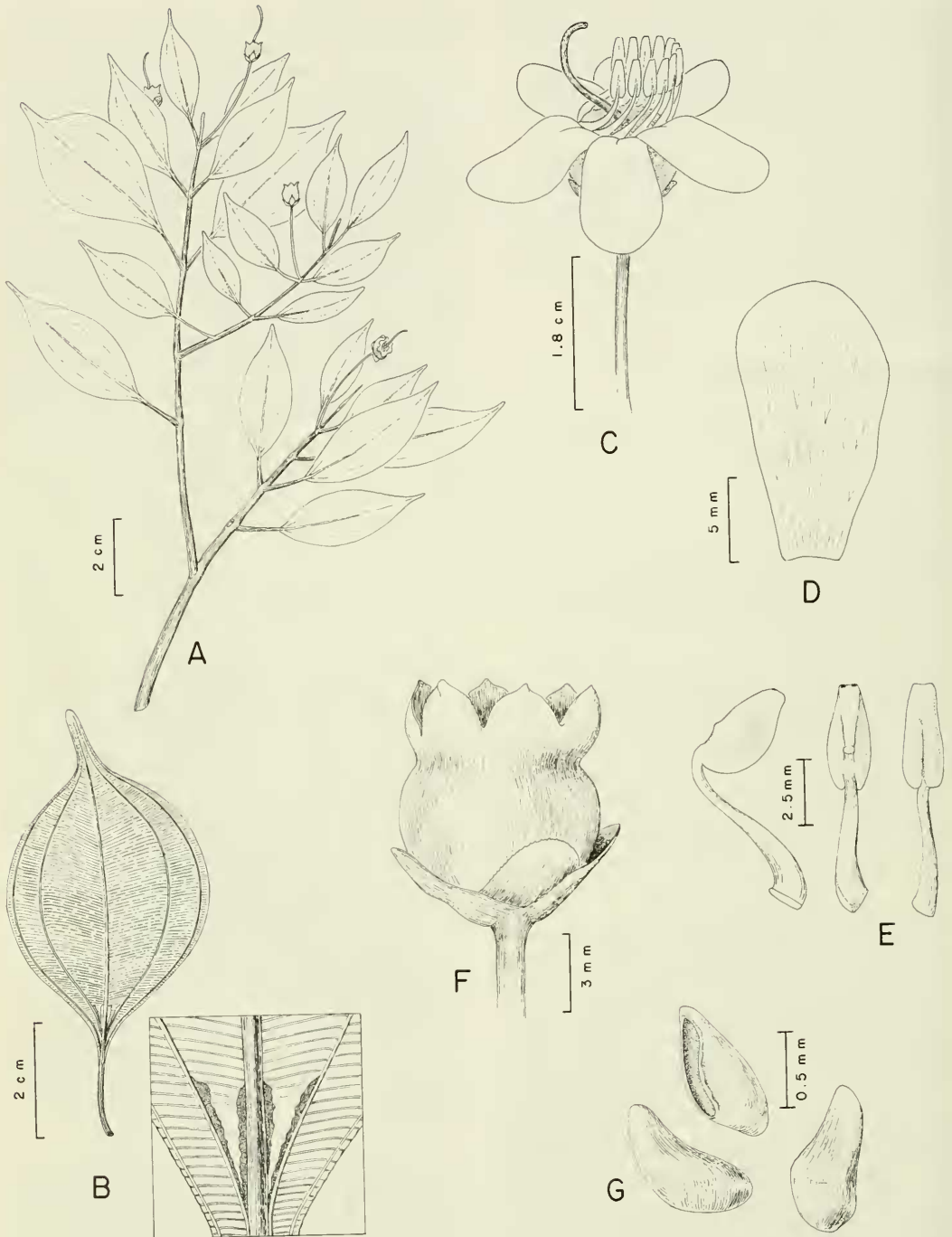


FIGURE 6. *Blakea hammelii* Almeda. A, habit; B, representative leaf with enlargement showing domatium (abaxial surface); C, representative flower (natural posture); D, petal (adaxial surface); E, stamens, lateral view (left), dorsal view (middle), ventral view (right); F, berry with persistent decussate bracts; G, seeds. (A, D, E from *Churchill & Kuijt 5103*; B from *Huft 1855*; C from *de Nevers & McPherson 6830*; F, G from *Schmalzel 1478*.)

Because of its elliptic to elliptic-ovate leaves with finely striolate secondary veins, erect long-pedicellate flowers, and white petals that are flushed with pink abaxially, *B. hammelii* is readily mistaken for *B. pauciflora* Gleason, to which it seems most closely related. The two differ primarily in androecial details and the nature of the calyx. In *B. pauciflora* the anthers, which are fused laterally for most of their length, are conic to rounded apically with two minute subterminal pores positioned on the ventral side of the anther sacs. Many specimens of *B. pauciflora* and *B. hammelii* are collected only in fruiting condition, but the flaring, essentially truncate, calyx of the former provides a consistent character by which the two species can be distinguished.

Although the domatia of *B. hammelii* and *B. pauciflora* are superficially similar to the pocket domatia of *Clidemia hammelii* Almeda (Almeda 1989), they appear to be modified versions of the pit or marsupiform (pocket-shaped) domatia described and illustrated by Jacobs (1966) and Stace (1965), respectively. The term domatium was coined by Lundström (1887) when he hypothesized a mutualistic relationship between mites and plants bearing these structures. Because of insufficient field study and the lack of experimental data, the functional significance of foliar domatia has remained conjectural for over a century. Based in part on Lundström's seminal paper, Pemberton and Turner (1989) recently presented new data to "support the hypothesis of a widespread facultative mutualism in which leaf domatia serve as shelters and nurseries for beneficial mites, which in turn reduce the number of phytophagous arthropods and pathogens using the plants." Interestingly, Pemberton and Turner found three genera of predaceous mites in 32% of the domatia of an unidentified Panamanian species of *Blakea* examined specifically for their study.

This species is named for Barry E. Hammel (1946–), avid student of the Mesoamerican flora, who collected the type of this and several other recently described species of Melastomataceae.

***Blakea herrerae* Almeda, sp. nov.**

(Fig. 7)

TYPE.—PANAMA. Comarca de San Blas: El Llano-Carti road at about km 19. Ina Igar trail in the vicinity of Nusagandi, elev. 350 m, 1 Feb. 1989, *Almeda et al.* 6507 (holotype: CAS!; isotypes: AAU!, BM!, BR!, CR!, DUKE!, F!, G!, MA!, MEXU!, MICH!, MO!, NY!, P!, PMA!, TEX!, US!, WIS!).

Frutex epiphyticus. Ramuli subquadrangulares demum teretes primum sicut folia novella obscure furfuracei mox glabrati. Petioli 1–2 cm longi; lamina 6.5–11 × 3.2–5.8 cm elliptica vel elliptico-obovata apice caudata vel cuspidata basi acuta, 3-nervata vel 3-plinervata, subcoriacea et integra, nervis secundariis 0.25 mm longis, lobis 1–2 mm longis. Flores 6-meri in quocumque nodo superiore 1–2(–3), pedicellis 0.5–1.2 cm longis, bractea omnino liberae; bractea exteriores 2.5–5 × 1.5–2.5 mm oblongo-lanceolatae acutae primum extus sparse vel modice subamorpho-furfuraceae demum glabratae; bractea interiores 2–4 × 2–3 mm ellipticae vel ovato-ellipticae apice late acuto extus glabrae. Hypanthium (ad torum) 3–4 mm longum extus sparsiuscule caduceque subamorpho-furfuraceum; calycis tubus 1.5–2.5 mm longus, lobis 1–2 mm longis. Petala 6–7 × 3–5 mm obovato-oblonga apice rotundato. Filamenta 3–4 mm longa; antherae 2.5–3 × 0.75–1 mm oblongae inter se lateraliter cohaerentes subapicaliter minute bipoosae; connectivum nec prolongatum nec appendiculatum. Stylus 6–7 mm; ovarium 6-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Epiphytic shrubs 2–4 m tall. Distal branchlets subquadrate, becoming rounded with age. Vegetative buds and very young leaves deciduously scurfy-puberulent. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout; petioles 1–2 cm long; blades subcoriaceous, 6.5–11 cm long and 3.2–5.8 cm wide, elliptic to elliptic-obovate, apex caudate to cuspidate or rarely varying to acuminate, base acute, margin entire, 3-nerved or 3-plinerved with an additional submarginal pair of inconspicuous veins, the striolate transverse secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade. Flowers erect, solitary or paired, rarely in fascicles of three in each leaf axil of the distal branches; pedicels 0.5–1.2 cm long, sparingly scurfy-puberulent to glabrous. Floral bracts sessile, entire, and free to the base; outer bracts 2.5–5 × 1.5–2.5 mm, oblong-lanceolate, apex acute, sparingly to moderately scurfy-puberulent to glabrate; inner bracts 2–4 × 2–3 mm, elliptic to elliptic-ovate, apex acute, essentially glabrous but fimbriolate-puberulent on the margins. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus and 3–4 mm in diameter, sparingly and deciduously scurfy-puberulent. Calyx tube 1.5–2.5 mm long; calyx lobes 1–2 mm long and 2.5–3 mm wide basally, triangular to triangular-ovate, margin entire or deciduously ciliate, glabrous on both surfaces. Petals 6, glabrous, 6–7 × 3–5 mm, pale greenish-white, oblong-obovate, apically rounded, entire. Stamens 12, isomorphic; filaments 3–4 mm long, complanate, glabrous and declined to one side of the flower opposing the style; anthers 2.5–3 mm long, 0.75–1 mm wide, yellow, laterally connate for their entire length,

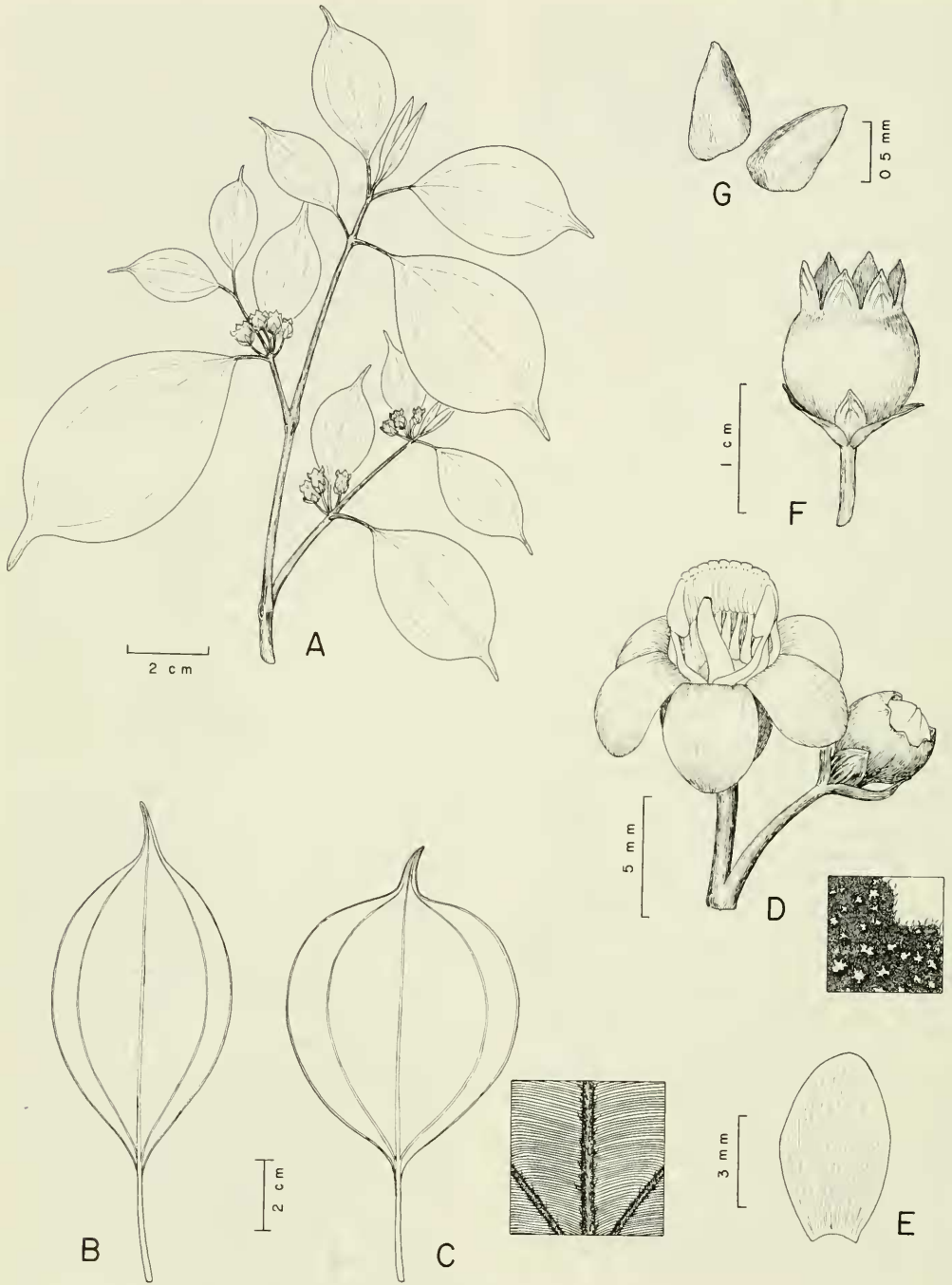


FIGURE 7. *Blakea herrerae* Almeda. A, habit; B, C, representative leaves (abaxial surface) showing variation in shape and enlargement (Coclé population) showing pubescence details; D, representative flower and bud (natural posture) with enlargement showing hypanthial pubescence; E, petal (adaxial surface); F, berry with persistent decussate bracts; G, seeds. (A-E from the holotype; F, G from *Sytsma et al.* 2603.)

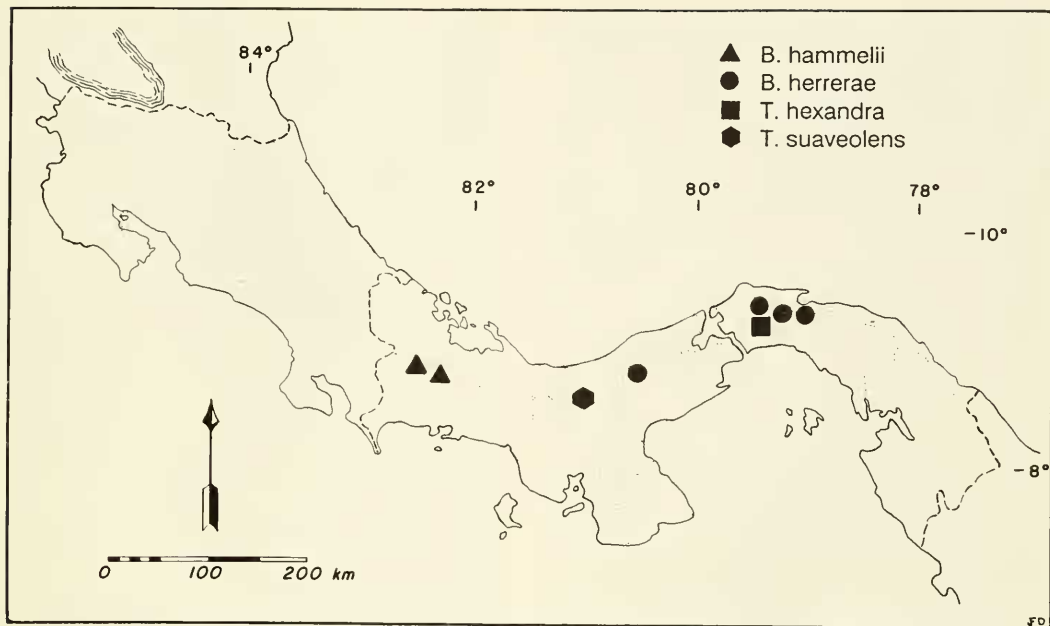


FIGURE 8. Distributions of *Blakea hammelii*, *B. herrerae*, *Topobea hexandra*, and *T. suaveolens*.

linear-oblong, with two minute pores positioned ventrally just below the truncate apex; connective slightly thickened dorsally but not prolonged or appendaged at the filament insertion. Ovary completely inferior, 6-celled, glabrous at the summit surrounding the stylar scar but not distended into a prominent cone or collar. Style somewhat declinate and slightly incurved distally, glabrous, 6–7 mm long; stigma truncate. Berry globose and pink at maturity, 9–10 mm long and 10–12 mm in diameter. Seeds clavate to narrowly pyriform or pyramideate, 1–1.5 mm long, beige with a smooth testa and conspicuous lateral raphe.

**PHENOLOGY.**—Flowering and fruiting occur sporadically throughout the year.

**DISTRIBUTION.**—Low rainforests from the Caribbean slope of central Panama (Coclé) east to the Llano-Cartí road in the Nusagandi region (Comarca de San Blas) at 100–400 m (Fig. 8).

**ADDITIONAL SPECIMENS EXAMINED.**—PANAMA. Coclé: between La Junta and Limón, 5 hr. walk N of Alto Calvario, 11 Oct. 1977, *Folsom 5878* (CAS); trail between Río Blanco and Continental Divide N of El Copé and El Petroso sawmill, 8°38'N, 80°36'W, 14 Dec. 1980, *Sytsma et al. 2603* (CAS). Comarca de San Blas: Llano-Cartí road, km 16, trail to creek on Atlantic drainage, 2 Feb. 1989, *Almeda et al. 6523* (CAS, PMA); Nusagandi, Llano-Cartí road, 28 Jul. 1984, *de Nevers & Todzia 3540* (CAS); along Llano-Cartí road, W of road 13.8

km to 15.8 km from Interamerican Hwy., 9°19'N, 78°55'W, 24 Aug. 1984, *de Nevers et al. 3746* (CAS); Llano-Cartí road, 13.8 km to 19 km from Interamerican Hwy., 9°19'N, 78°55'W, 3 Sep. 1984, *de Nevers & Porras 3822* (CAS); Llano-Cartí road, km 19.1, 9°19'N, 78°56'W, 9 Nov. 1984, *de Nevers & Herrera 4242* (CAS); Llano-Cartí road, km 19.1, 9°19'N, 78°55'W, 11 Mar. 1985, *de Nevers & Herrera 5100* (CAS). Comarca de San Blas/Panama Border: on Kuna divide trail N of Llano-Cartí road, 9°20'N, 79°00'W, 16 Dec. 1987, *McPherson 11879* (MO). Panama: Llano-Cartí road, 9°16'N, 78°58'W, 12 Sep. 1980, *Sytsma 1077* (CAS); headwaters of Río Chagres, Río Esperanza, and Río Piedras, 9°20'N, 79°20'W, 17 Oct. 1984, *de Nevers et al. 4088* (CAS).

First collected in 1977, *Blakea herrerae*, is another species that has been confused with, and is probably derived from, *B. pauciflora*. Both species have finely striolate secondary foliar venation and laterally fused anthers that are declined to one side of the flower to form a semicircle. *Blakea pauciflora* differs from *B. herrerae* in a number of floral characters. The pedicels of *B. pauciflora* are longer (2.5–5.3 cm), the calyx is essentially truncate and flaring, the style is longer (9–12 mm) and flexuous, and the larger petals (13–19 × 8–10 mm) are white flushed with pink instead of pale greenish-white. *Blakea herrerae* is also distinctive in that some mature leaves on all collections examined have cryptic tufts of short stiff hairs on the lower surface in the angles between the median vein and each of the two

proximal lateral veins. These may well function as acarodomatia, like the concentrated foliar hair tufts now known to harbor beneficial mites in many plant groups (Pemberton and Turner 1989).

There is some variation in the size and shape (Fig. 7B, C) of mature leaves, but none of this can be correlated with geography, elevation, or other diagnostic characters. Despite the limited range of this species, there is some variation that appears to be geographically correlated. The two cited collections from Coclé Province west of the Canal Area (Fig. 8) differ from populations east of the Canal in having elevated primary leaf veins below that are sparsely beset with a mixture of scurfy hairs and spreading glandular hairs. The lower leaf surfaces of these two collections are also unusual in having a liberal scattering of minute red glands on and between the striolate secondary veins. More material from Coclé and other intervening areas is needed to better assess the significance of these differences in pubescence.

A population from Cerro Jefe, Panama (represented by *D'Arcy 12181*, *McPherson 7435*, and *Sytma 1414*, all CAS), is similar to *B. herrerae* in foliar venation, details of the floral bracts, and anther morphology. These collections differ from other cited material in having thicker leaves, larger petals (12–15 × 8–9 mm) that are pink, and longer styles (11–12 mm long). Because plants of this population differ from typical specimens of *Blakea herrerae* in characters that are commonly diagnostic, they are excluded from my circumscription of this species pending additional study.

Field study of this species in the Nusagandi region revealed an unusual method of vegetative reproduction that to my knowledge has never been reported for an epiphytic member of the Melastomataceae. *Blakea herrerae* is commonly a massive rainforest epiphyte with lax spreading branches that skirt host trees. In two individuals examined, the outermost branches were attached to adjacent trees by clinging adventitious roots. One individual had colonized four neighboring host trees in this fashion.

*Blakea herrerae* also appears to be unique among the erect-flowered species of the genus in having greenish-white flowers that produce a pleasant spicy fragrance but lack nectar. The fragrance is reminiscent of that produced by neotropical orchids that are pollinated by male euglossine bees. The few species of *Blakea* and *Topobea* with showy white and/or pink flowers

that have been studied in the field are buzz-pollinated by many species of bees (including two euglossine genera) seeking pollen as a floral reward (Lumer 1981; Renner 1989). Several euglossine genera are among the common buzz-pollinating bees in the neotropics (Buchmann 1983; Roubik 1989). However, only female euglossines are known to collect pollen from neotropical Melastomataceae (Renner 1989). In the male euglossine pollination syndrome of the Orchidaceae, the flowers produce no nectar and the pollen is not available as a food source. It will be interesting to learn if euglossine bees buzz-pollinate the poricidal anthers of *B. herrerae* and if its floral fragrance serves only as a secondary attractant, as suggested by Renner (1989) for melastomes in general. In addition to the Orchidaceae, floral fragrance collection by male euglossines has been found in some species of *Anthurium* and *Spathiphyllum* (both in the Araceae), one species of *Gloxinia* (Gesneriaceae), *Cyphomandra* (Solanaceae), *Dalechampia* (Euphorbiaceae), and a scattering of species in other families of flowering plants (Ackerman 1986; Williams 1983). Because pollen presentation in *Cyphomandra* provides a parallel to the poricidally dehiscent anthers of *Blakea herrerae*, additional fieldwork is needed to document details of its pollination biology.

This species is named for Heraclio Herrera (1959–), a student of the Panamanian flora who kindly directed me to a flowering population of this species at Nusagandi, Panamá.

### ***Blakea scarlatina* Almeda, sp. nov.**

(Fig. 9)

TYPE.—COSTA RICA. Alajuela: 20–30 km SE of Cataratas de San Ramón, elev. 2,150–2,500 ft. (655–762 m), 20 Mar. 1978, *Almeda et al. 4308* (holotype: CAS!).

Frutex epiphyticus ca. 4 m altus. Ramuli primum subquadragulati demum teretes sicut folia novella pedicelli hypanthiaque sparse vel densi furfuracei demum glabrati. Petioli 1.7–4.5(–6.3) cm longi; lamina 8.5–19.7 × 5.4–10 cm elliptica vel elliptico-ovata apice acuminata basi acuta vel obtusa vel rotundata, 3-nervata, coriacea et integra, nervis secundariis 1–2 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli, pedicellis 1–1.8 cm longis; bractee exteriores 2–2.7 × 2.2–3.6 cm late ovatae vel suborbiculares ca. 1–1.5 cm coalitae apice truncato-rotundato plerumque mucronato; bractee interiores 1–2 cm omnino coalitae. Hypanthium (ad torum) 1–1.3 cm longum; calycis tubus 5–6 mm longus, lobis 5–10 mm longis. Petala 3–4.5 × 2.5–4.3 cm obovata vel cuneata apice truncato vel rotundato. Filamenta 9–13 mm longa; antherae 6–8 × 4–6 mm inter se non coherentes, poris duobus minutis terminalibus; connectivum ad basim dorsaliter dente



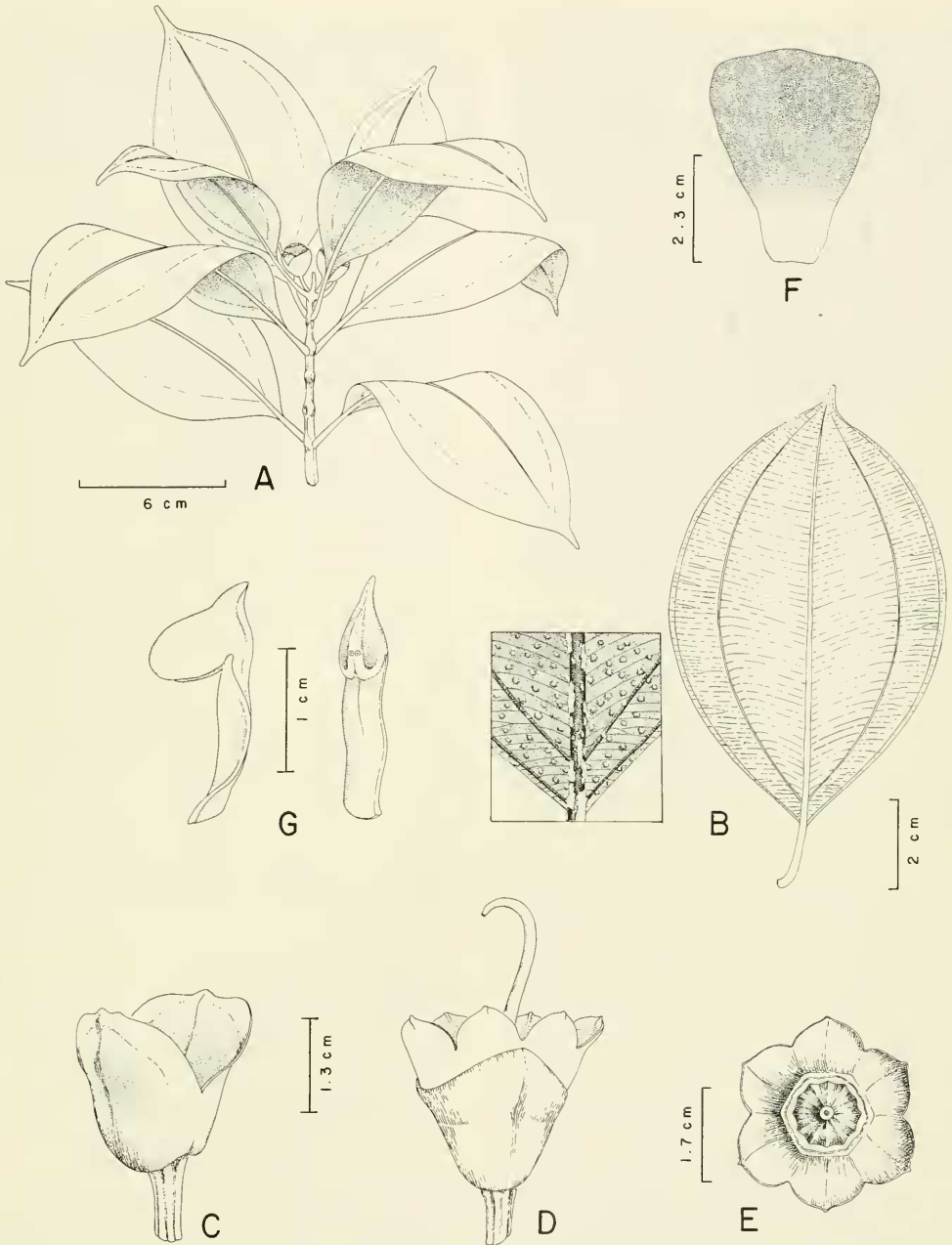


FIGURE 9. *Blakea scarlantina* Almeda. A, habit; B, representative leaf (abaxial surface) with enlargement showing pubescence detail; C, outer floral bracts; D, inner floral bracts enveloping hypanthium; E, hypanthium (top view) showing ovary summit, torus and calyx lobes; F, petal (adaxial surface); G, stamens, lateral view (left), ventral view (right). (A, B from the holotype; C-G from *Hammel 9297*, CAS.)

3-5 mm armatum. Stylus 2-2.1 cm; ovarium 6-loculare et omnino inferum cono 5 mm longo (collo incluso) glabro.

Massive epiphytic shrubs to 4 m tall with coarse spreading branches 0.5-8 m long. Vegetative

buds, juvenile leaves, pedicels, and young hypanthia sparsely to densely furfuraceous-puberulent but becoming glabrate with age. Mature leaves of a pair essentially equal or only slightly

unequal in size; petioles 1.7–4.5(–6.3) cm long; blades thick and coriaceous, 8.5–19.7 cm long and 5.4–10 cm wide, elliptic to elliptic-ovate, apex acuminate, base acute to obtuse or rounded, margin entire, 3-nerved with an additional pair of inconspicuous intramarginal veins, the transverse secondary veins mostly 1–2 mm apart at the widest portion of the blade, essentially glabrous but whitish punctulate above, sparsely furfuraceous-puberulent on the elevated primary veins below or almost glabrous. Flowers erect, solitary in the axils of uppermost leaves; pedicels somewhat compressed, 1–1.8 cm long. Floral bracts thick and coriaceous, sessile and entire; outer bracts connate basally for about half their length, 2–2.7 × 2.2–3.6 cm, broadly ovate to suborbicular, apex rounded to subtruncate, typically mucronate, deciduously furfuraceous-puberulent abaxially; inner bracts connate for their entire length to form a shallowly lobed, glabrous, bowl-like collar 1–2 cm high that envelops the hypanthium but is usually concealed by the outer bracts. Hypanthia (at anthesis) campanulate, 1–1.3 cm long to the torus and 1.3–1.6 cm in diameter. Calyx tube 5–6 mm long; calyx lobes erect or slightly spreading, 5–10 mm long and 9–14 mm wide basally, triangular-ovate and apiculate, margin entire, moderately to sparingly furfuraceous-puberulent abaxially. Petals 6, fleshy and glabrous when fresh, 3–4.5 × 2.5–4.3 cm, brilliant red but white for the basal ¼ of their length, obovate to cuneate, apically truncate to broadly rounded, entire. Stamens 12, isomorphic, free but connivent and forming a somewhat declinate nearly semicircular ring around the style; filaments complanate, white, fleshy and glabrous, 9–13 mm long; anthers 6–8 mm long and 4–6 mm wide, yellow, oblong-ovoid, laterally compressed and tipped with two minute pores; connective thickened and prolonged dorsally at the base into an acute spur 3–5 mm long that assumes a pseudoterminal position because of the pronounced adaxial tilt of each anther apex. Ovary completely inferior, 6-celled, glabrous at the gently fluted summit and dilated apically into a cone and stylar collar 5 mm long. Style declinate and incurved distally, glabrous, 2–2.1 cm long and 0.5–1 mm wide, stigma truncate to capitate. Mature berry and seeds not seen.

**PHENOLOGY.**—Flowering specimens have been collected in every month except December and January; of the nearly 40 collections available for this study none had mature fruits.

**DISTRIBUTION.**—Widespread but local and uncommon in wet evergreen forests from southern Nicaragua (Zelaya) south to Costa Rica from Parque Nacional Rincón de la Vieja (Guanacaste) and the Cordillera de Tilarán (Alajuela) southeast to the vicinity of Turrialba (Cartago) from sea level to 1,450 m (Fig. 5).

**ADDITIONAL SPECIMENS EXAMINED.**—COSTA RICA. Alajuela: 3 km N of Río Cataratas on road to Bajo Rodríguez, 23 Feb. 1978, *Almeda & Nakai 3884* (CAS, CR); 18–35 km NNW of San Ramón on road to Cataratas, 21 Mar. 1986, *Almeda et al. 5652* (CAS); La Palma de San Ramón, 6 Nov. 1923, *Brenes 3920* (F); La Palma de San Ramón, 29 Sep. 1925, *Brenes 4466* (F); La Palma de San Ramón, 24 Oct. 1926, *Brenes 5031* (F); La Palma de San Ramón, 24 Nov. 1926, *Brenes 5115* (F); La Palma de San Ramón, 24 Nov. 1926, *Brenes 5138* (F); La Palma de San Ramón, 22 Aug. 1927, *Brenes 5671* (F); La Palma de San Ramón, 5–8 Aug. 1935, *Brenes 20627* (F); Reserva Forestal de San Ramón above and in valley of Río San Lorencito, 10°13'N, 84°37'W, 12–14 Mar. 1987, *Burger et al. 12105* (CAS, F); Monteverde Reserve, Atlantic slope, Río Peñas Blancas valley, 19 Mar. 1986, *Haber 1519* (CAS); San Carlos, margin of Río Peñas Blancas at elevation of San Pedro, 29 Jun. 1985, *Haber & Bello 1744* (CAS); San Carlos, Peñas Blancas, 9 Jul. 1985, *Haber & Bello 1873* (CAS); Río Peñas Blancas, San Carlos, 11 Aug. 1985, *Haber & Bello 2306* (CAS); finca Don Bolívar Ruiz on road between the Reserva de San Ramón station and the road to Palmareña, Feb. 1987, *Herrera 508* (CAS); 6 km S of Ciudad Quesada, near Río La Vieja, 10 Sep. 1967, *Lent 1265* (F); 8 km NE of Villa Quesada, near Artezalea, 17 Feb. 1966, *Molina et al. 17258* (F); near San Isidro de Peñas Blancas, 22 Oct. 1965, *Schnell 231* (F); La Marina, near Ciudad Quesada, 23 Oct. 1965, *Schnell 243* (F); Villa Quesada, 21 Feb. 1939, *Smith III603* (F); 5.8 km N of Cataratas de San Ramón, 11 Apr. 1976, *J. & K. Utley 4606* (CAS, DUKE). Cartago: Instituto Interamericano de Ciencias Agrícolas, Turrialba, 4 Oct. 1950, *León 2790* (MO); 2.5 km E of Tuis along banks of Río Tuis, 9 Mar. 1978, *Utley 6006* (CAS, DUKE). Cartago/San José Border: Estación Carrillo, Parque Nacional Braulio Carrillo, 28 Jul. 1984, *Zamora & Elizondo 672* (CAS). Guanacaste: Parque Nacional Rincón de la Vieja, Hacienda Santa María, SE of Mirador on road to Volcán Santa María, 10°48'N, 85°19'W, *Herrera & Robles 756* (CAS, MO). Heredia: Finca La Selva on Río Puerto Viejo, just E of its junction with the Río Sarapiquí, along Far Loop Trail, 1,000 m S, 21 Jul. 1980, *Hammel 9297* (CAS, DUKE, F); Finca La Selva on Río Puerto Viejo just E of its junction with Río Sarapiquí, ridge above Q. Esquina, 30 Aug. 1981, *Smith 135* (CAS, DUKE). Limón: hills 2 airline km SSE of Islas Buena Vista in Río Colorado, 10°40'N, 83°40'W, 13–14 Sep. 1986, *Davidse & Herrera 31127* (CAS); Hacienda Tapezcó-Hda. La Suerte, 29 airline km W of Tortuguero, 10°30'N, 83°47'W, 28 Aug. 1979, *Davidson & Donahue 8913* (CAS); path beyond Río Sucio, Braulio Carrillo, May 1984, *Gomez et al. 22760* (CAS); ridge between Río Chirripó and Q. El Molinete, 10°12'N, 83°54'W, 19 Jul. 1984, *Grayum et al. 3553* (CAS); Cerro Coronel, E of Laguna Danto, 10°41'N, 83°38'W, 15–20 Sep. 1986, *Stevens & Montiel 24614* (CAS). Puntarenas: Monteverde community, windbreak next to road, 10°20'N, 84°50'W, 22 Jul. 1986, *Haber 5729* (CAS). NICARAGUA. Zelaya: 4 km N of Nueva Guinea, between Río Plata and San Antonio, 11°44'N, 84°26'W, 7 Sep. 1983, *Neer 27883* (CAS).

*Blakea scarlatina* is unique among its Central American congeners in having large flowers (8–9 cm across at anthesis) with brilliant red petals that are white for the basal ¼ of their length. For an obligate epiphyte this species has a comparatively broad geographic and elevational distribution; however, all available collections exhibit remarkable uniformity in floral and vegetative features.

*Blakea scarlatina* was first collected by A. M. Brenes in 1923. Many additional specimens have accumulated in herbaria since that time, but most have repeatedly been misidentified as *B. grandiflora* Hemsley. *Blakea grandiflora*, which is known only from higher elevations (1,400–2,350 m) in Costa Rica, differs in having 5-plinerved leaves with an additional intramarginal pair of veins, longer pedicels (3–5 cm), flowers borne in clusters of 2–4 in the upper leaf axils, petals that are white flushed with pink distally, and anther connectives that are modified dorso-basally into short deflexed spurs. Vegetatively, *B. scarlatina* has an aspect most reminiscent of *B. cuneata* Standley, a little-collected species of Belize, Guatemala, and Honduras. Striking similarities in foliar morphology and pubescence details initially led me to assign many collections of *B. scarlatina* to *B. cuneata*. Study of the type of *B. cuneata* and more recent collections, however, leaves no doubt that these two allopatric species are readily separated by a number of diagnostic characters. In *B. cuneata* there is a consistent tendency for the elliptic leaves to be narrower (3.5–6 cm), and the free portions of the outer floral bracts are elliptic-lanceolate and bluntly acute at the apex. *Blakea cuneata* also differs in having smaller petals (1.8–2.1 × 1.5–2 cm) that are pink, shorter filaments (5–6 mm), and linear-oblong anthers that are short (5–5.5 mm), erect, and unappendaged dorso-basally.

In anther morphology *B. scarlatina* most closely approaches *B. tuberculata* J. D. Smith and *B. cuatrecasii* Gleason. *Blakea tuberculata* also has anthers that are connivent and free, but they form a complete circle around the straight style. *Blakea cuatrecasii* has stamens that form a nearly circular ring opposing the declinate style, but the anthers are laterally fused for nearly half of their length. Because both of these species differ from *B. scarlatina* in so many other characters, I see no compelling reason to suggest that they form a particularly close alliance based solely on androecial morphology.

The flowers of *B. scarlatina* are some of the most spectacular among neotropical epiphytes. They are also some of the most enigmatic when attempting to make inferences about likely pollinators. The casual observer might be inclined to suggest bird pollination because of the brilliant red coloration of the petals. This seems highly unlikely. I have found no detectable nectar in any flowers examined in the field during morning and late afternoon hours. These observations are supported by Stein and Tobe (1989), who found no anatomical basis for nectar production in this species (referred to as *Blakea* sp. nov.).

Although pollinators of *B. scarlatina* remain unknown, a color slide photograph in the fragment packet of Burger *et al.* 12105 shows the brown anther discoloration (bruising) typically found on yellow-anthered melastome species that have been visited by buzz-pollinating bees. Field studies will be needed to determine the pollinator spectrum of this species and to evaluate conflicting reports on the nature of its floral fragrance. The flowers of *B. scarlatina* have been described as having a musky odor (Haber 1519), a distinct delicate fragrance (Almeda *et al.* 5652), and a strange, unpleasant odor (Nee 27883).

The name for this species is derived from *scarlatinus*, Latin for scarlet, in reference to the vivid red petal color.

### *Topobea caliginosa* Almeda, nom. nov.

*Blakea micrantha* Almeda, Rhodora 82:614. 1980.

TYPE.—PANAMA. Veraguas: Cerro Tute ca 10 km NW of Santa Fe on ridgetop in cloud forest above 1,000 m, 19 Jun. 1975, Mori 6765 (holotype: CAS!; isotype: MO!).

A study of anther morphology in recently collected flowering material of this species has led to the conclusion that it is closely related to *T. cordata*, *T. crassifolia*, and *T. hexandra*. This has necessitated a reassessment of the proper generic placement for this specialized group of species. For reasons discussed in the synoptic history at the beginning of this paper, it seems appropriate to transfer *Blakea micrantha* to *Topobea*. Adoption of a nomen novum is needed because the epithet *micrantha* is pre-empted in *Topobea* (Almeda 1981b:307). For additional comments and an enumeration of its diagnostic features, see the discussion under *T. hexandra*. The new name for this species is derived from *caligo*, Latin for fog, mist, or darkness, in reference to its fog-shrouded habitat at the summit of Cerro Tute.

**Topobea crassifolia** (Almeda) Almeda, comb. nov.

*Blakea crassifolia* Almeda, *Rhodora* 82:612. 1980.

TYPE.—PANAMA. Coclé: La Mesa above El Valle in forest on both sides of junction with road to Cerro Pilón, ca 800 m, 21 Jul. 1974, *Croat 25430* (holotype: CAS!; isotypes: MO!, US!).

The rationale for transferring *B. micrantha* to *Topobea* also applies to *B. crassifolia*. Among the four hexandrous species, *T. crassifolia* is most like *T. cordata* in having ovate to elliptic-ovate leaves and a 4-celled ovary. The leaves of *T. crassifolia* are petiolate whereas those of *T. cordata* are invariably sessile. Another difference between these two species are discussed above under the synoptic history. With a distribution that extends to Costa Rica, *T. crassifolia* is the only hexandrous species known to occur outside of Panama.

**Topobea fragrantissima** Almeda, sp. nov.

(Fig. 10)

TYPE.—PANAMA. Chiriquí: vicinity of Fortuna Dam, along trail across valley of Río Hornito, elev. 1,100–1,250 m, 12 Mar. 1988, *Almeda et al. 6086* (holotype: CAS!; isotypes: CR!, F!, MO!, PMA!, TEX!, US!).

Frutex epiphyticus vel terrestris. Petioli 0.5–3 cm longi; lamina 1.5–5.5 × 1.6–3 cm elliptica vel elliptico-obovata apice acuminata basi acuta ad maturitatem glabra, 3-nervata vel 3-plinervata, subcoriacea et integra nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri in quoque nodo superiore singuli vel bini, pedicellis 2–3 cm longis, bracteae omnino liberae ellipticae vel obovatae; bracteae exteriores 5–11 × 3–5 mm apice rotundato; bracteae interiores 4–6 × 4–5 mm apice rotundato. Hypanthium (ad torum) 3–4 mm longum extus glabrum; calycis tubus 1 mm longus, lobis 1 mm longis. Petala 1.2–1.4 × 1–1.2 cm obovato-oblonga apice rotundato. Filamenta 5–6 mm longa; antherae 3.5–5 × 1 mm oblongae lateraliter non cohaerentes, poro unico dorsaliter inclinato; connectivum ad basim dorsaliter dente 0.25 mm longo descendenti armatum. Stylus 1–1.1 cm; ovarium 4-loculare et ½ inferum apice glabro (cono et collo non evoluto).

Epiphytic or terrestrial shrubs or small trees 1.5–4 m tall. Distal branchlets subquadrate and glabrous with interpetiolar ridges or lines. Vegetative buds and young leaves sparingly and deciduously lepidote-furfuraceous. Mature leaves of a pair equal to somewhat unequal in size, glabrous throughout; petioles 0.5–3 cm long; blades subcoriaceous, 1.5–5.5 cm long and 1.6–3 cm wide, elliptic to elliptic-obovate, apex acuminate, base acute, margin entire, 3-nerved or 3-plinerved abaxially with an additional submarginal pair of inconspicuous veins, the striolate transverse secondary veins spaced mostly 0.25

mm apart at the widest portion of the blade. Flowers erect, solitary or paired in leaf axils of distal branches; pedicels 2–3 cm long, glabrous. Floral bracts sessile, entire and free to the base; outer bracts 5–11 × 3–5 mm, elliptic or rarely varying to obovate, glabrous, apex rounded; inner bracts 4–6 × 4–5 mm, obovate, glabrous, apex broadly rounded. Hypanthia (at anthesis) campanulate, 3–4 mm long to the torus and 4–5 mm in diameter, glabrous. Calyx tube 1 mm long; calyx lobes 1 mm long and 1–1.5 mm wide basally, ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire but sometimes roughened along interlobe sinuses, glabrous on both surfaces. Petals 6, glabrous, 1.2–1.4 × 1–1.2 cm, white flushed with pink unilaterally, obovate, apically rounded, entire. Stamens 12, isomorphic, free and strongly declined to one side of the flower opposing the style; filaments campanulate and glabrous, 5–6 mm long; anthers 3.5–5 mm long, 1 mm wide, yellow, linear-oblong and tipped with a solitary dorsally inclined pore; connective dilated dorso-basally into a deflexed spur 0.25 mm long. Ovary ½ inferior, 4-celled, glabrous at the summit but not distended into a cone or collar. Style declinate and somewhat sigmoid, glabrous, 10–11 mm long; stigma punctiform. Berry globose, 7–10 mm long and 10 mm in diameter. Seeds clavate to narrowly pyriform or pyramidal, 1 mm long, beige with a smooth testa and conspicuous lateral raphe.

PHENOLOGY.—Flowering and fruiting specimens have been collected in January, March, April, and July.

DISTRIBUTION.—Local and uncommon in cloud forests from the Boquete region of western Panama (Chiriquí) to the slopes bordering the Río Hornito above Los Planes east to Cerro Colorado at 1,000–1,300 m (Fig. 5).

ADDITIONAL SPECIMENS EXAMINED.—PANAMA. Chiriquí: Edwin Fabrega Dam and Reserve along trail to Río Hornito above Los Planes, 8°45'N, 82°15'W, 18 Jan. 1989, *Almeda et al. 6309* (CAS, MO, PMA); Monte Rey, above Boquete, 21 Jul. 1971, *Croat & Porter 15692* (CAS, MO); trail to Zarzo, between Los Planes de Hornito and Fortuna Lake, 8°41'N, 82°13'W, *Hampshire & Whiteford 689* (BM, CAS); ca. 5 km E of Fortuna Dam along trail crossing Río Hornito, 8°45'N, 82°15'W, 26 Apr. 1988, *Thompson 5021* (CAS, CM). Chiriquí/Bocas del Toro Border: windswept cloud forest off the road to Cerro Colorado, 26 Jan. 1989, *Almeda et al. 6418* (CAS, CR, DUKE, MO, PMA, US).

*Topobea fragrantissima* is distinguished by its glabrous leaves with finely striolate secondary

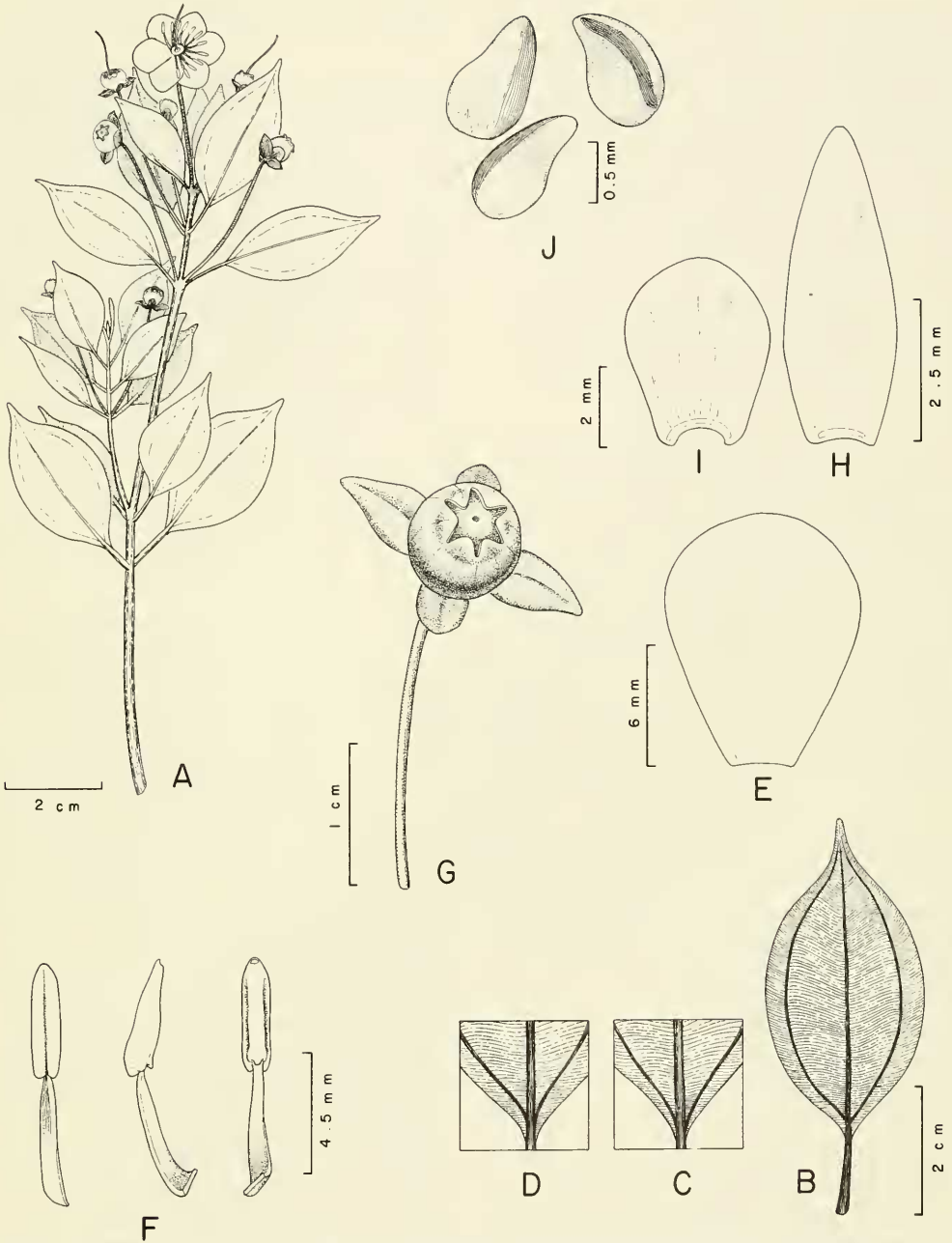


FIGURE 10. *Topobea fragrantissima* Almeda. A, habit; B, representative leaf (abaxial surface); C, D, enlargement of foliar venation (abaxial surface); E, petal (adaxial surface); F, stamens, ventral view (left), lateral view (middle), dorsal view (right); G, berry with persistent decussate bracts; H, outer floral bract (adaxial surface); I, inner floral bract (adaxial surface); J, seeds. (A-I from the holotype; J from *Croat & Porter 15692*, CAS.)

venation, long-pedicellate, erect flowers, linear-oblong anthers with solitary dorsally inclined pores, and a 4-celled ovary. Although it has been described as an epiphytic shrub or small tree, my

field observations and the label information on most collections suggest that this species typically becomes a small, free-living tree. The style in this species is declinate like many other species

of *Topobea*, but the posture and orientation of its androecium is unlike that of other congeners with free anthers. In the erect-flowered species of *Topobea* with free anthers, the filaments are declined to one side of the flower opposing the style and the anthers are typically erect or somewhat incurved apically. In *T. fragrantissima* this orientation is taken to such an extreme that both filaments and anthers lie flat on the surface of the petals to form a semicircular configuration (Fig. 10A). In this unusual androecial orientation the ventral surface of the anther faces upward and the dorsal surface (including the dorsally inclined pore) face downward toward the petal surface.

Field observations of pollination in this species should be of special interest because this pollen presentation mechanism is coupled with the production of a perfume-like fragrance. The unusual anther posture and orientation of the pore may require some peculiar manipulative behavior on the part of bees if this species is buzz-pollinated like the majority of species in the family with poricidally dehiscent anthers.

*Topobea fragrantissima* is similar to *T. suaveolens* (also described below) in a number of characters, and it seems likely that these two species are closely related. The shape and venation of mature leaf blades are nearly identical. In the few known collections of *T. suaveolens*, however, foliar pocket domatia (Fig. 12B) are formed abaxially in the angle between the median vein and the innermost pair of lateral veins; domatia are lacking in *T. fragrantissima*. The differences between these species are most readily apparent when fresh flowers are examined. In *T. suaveolens* the connivent petals give the pendant flowers a bell-like conformation, the free stamens form a ring around the straight style, and the ovary is 6-celled. The most distinctive feature shared by the two species is the solitary anther pore. Within the Blakeeae, this derived character is known in other species. *Topobea acuminata* Wurdack, *T. caudata* Wurdack, *T. dodsonorum* Wurdack, and *T. pittieri* Cogn. are a few notable examples. The fact that solitary anther pores occur in more than one species complex within *Topobea* suggests that this character has arisen more than once in the course of its evolutionary history.

The name for this species is derived from *fragro*, Latin for sweet smelling, in reference to the perfume-like fragrance of fresh flowers.

### *Topobea hexandra* Almeda, sp. nov.

(Fig. 11)

TYPE.—PANAMA. Panamá: Cerro Jefe, along summit road and along trail into the Chagres Valley, elev. ca. 900 m, 19 Feb. 1988, *Almeda et al.* 5837 (holotype: CAS!; isotypes: CR!, DUKE!, F!, MO!, NY!, PMA!, TEX!, US!).

Frutex hemiepiphyticus. Ramuli primum sulcato-quadrangulati demum teretes glabri (in nodis caduce puberuli pilis castaneis ca. 0.5–1 mm longis). Petioli 5–14 mm longi; lamina 2–3.9 × 1.1–3 cm subrotundata vel elliptico-ovata apice rotundato vel obtuso basi late acuta vel obtusa vel rotundata, 3-nervata coriacea et integra, nervis secundariis nervulisque invis. Flores 6-meri sessiles vel subsessiles in quoque nodo superiore singuli vel bini; bractae omnino liberae; bractae exteriores 5–6.5 × 3–5 mm ovatae vel ovato-ellipticae apice obtuso vel mucronato; bractae interiores 4–5 × 4–6 mm late ovatae vel suborbiculares apice rotundato. Hypanthium (ad torum) 3 mm longum extus sparsiuscule caduceque stellulato-furfuraceum; calycis tubus 1 mm longus, lobis 2 mm longis. Petala 6.5–7 × 4 mm obovato-elliptica apice obtuso. Filamenta 3 mm longa; antherae 6, ca. 2 × 1 mm oblongae inter se non cohaerentes, ventraliter biporosae; connectivum ad basim dorsaliter dente 0.25 mm descendenti armatum. Stylus 5.5 mm; ovarium 2-loculare et omnino inferum apice glabro (cono et collo non evoluto).

Hemiepiphytic shrubs to 1 m tall adhering to the bark of host trees by nodal and internodal adventitious roots. Distal branchlets quadrate to quadrisulcate, glabrous or sparsely beset with spreading, deciduous, glandular hairs 1–2 mm long like the young petioles and upper and lower surfaces of the juvenile leaves; older branches rounded with leaf scars that are typically swollen and nodular in appearance. Uppermost nodes copiously beset with brown spreading hairs. Vegetative buds copiously covered with a deciduous brown stellate-lepidote indument. Leaves of a pair equal in size, glabrous throughout; petioles 5–14 mm long; mature blades coriaceous, 2–3.9 cm long and 1.1–3 cm wide, suborbicular to elliptic-ovate, apex rounded or varying to obtuse, base obtuse to rounded, rarely varying to acute, margin entire, 3-nerved, often with an additional intramarginal pair of depressed veins. Flowers erect, solitary or paired in the leaf axils of distal branches, sessile or subsessile with short (to 1 mm) ill-defined pedicels formed by the compressed bases of the outer floral bracts. Floral bracts thick and semisucculent, sessile, entire and free to the base, sparingly stellulate-furfuraceous abaxially; outer bracts 5–6.5 × 3–5 mm, concave, ovate to elliptic-ovate, apex obtuse to bluntly mucronate; inner bracts 4–5 × 4–6 mm, broadly ovate to suborbicular, apex rounded. Hypanthia (at anthesis) narrowly campanulate,

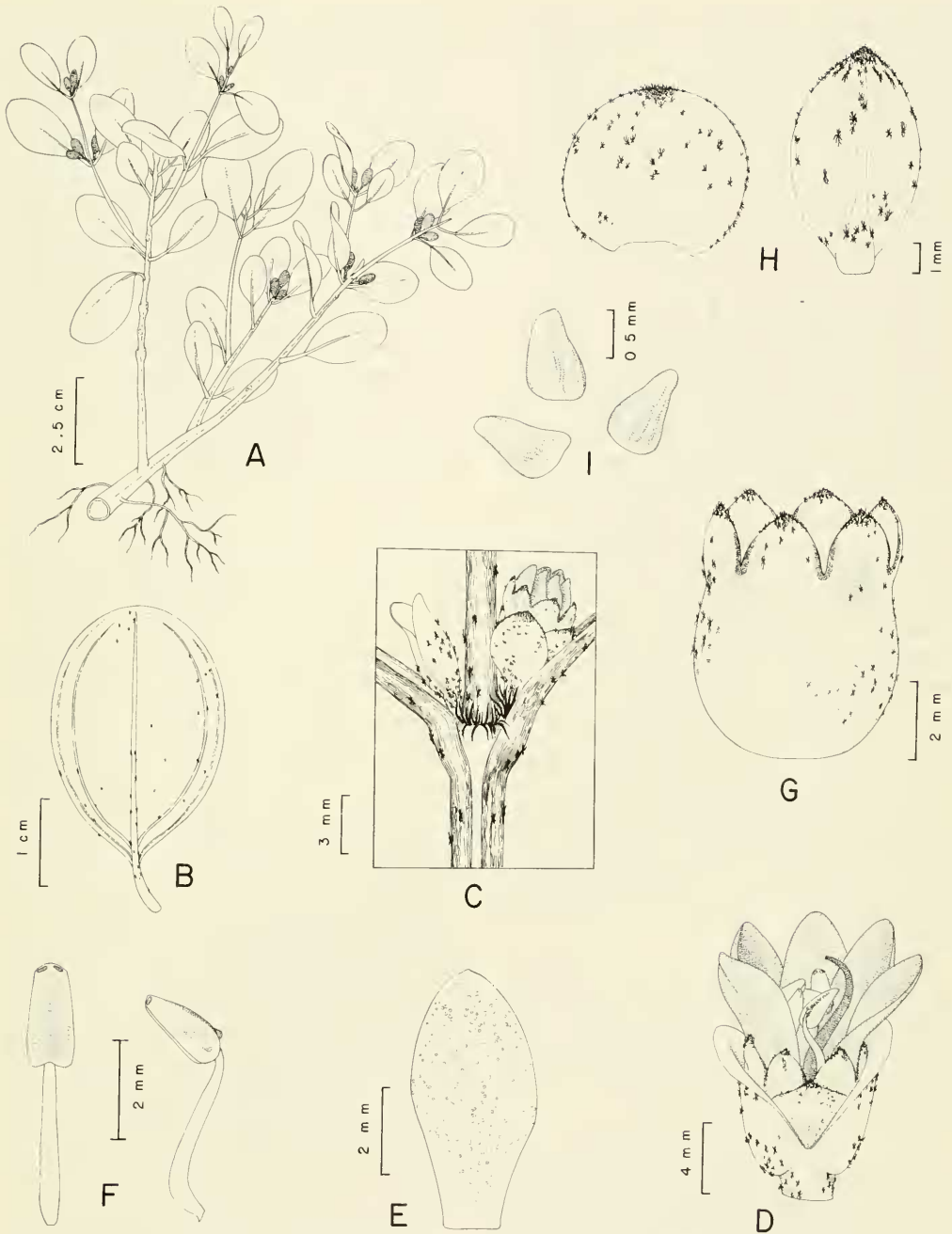


FIGURE 11. *Topobea hexandra* Almeda. A, habit; B, representative leaf (abaxial surface), C, enlargement of distal node showing spreading hairs; D, representative flower (natural posture); E, petal (abaxial surface); F, stamens, ventral view (left), lateral view (right); G, berry with persistent floral bracts removed; H, abaxial surface of inner floral bract (left), abaxial surface of outer floral bract (right); I, seeds. (A–H from the holotype; I from *Witherspoon 8552*.)

3 mm long to the torus and 4–5 mm in diameter, sparingly stellate-lepidote or stellulate-furfuraceous. Calyx tube 1 mm long; calyx lobes erect, 2 mm long and 2–2.5 mm wide basally, ovate to deltoid-ovate, entire but irregularly roughened along interlobe sinuses, sparingly stellate-lepidote. Petals 6, liberally covered with disc-shaped hyaline processes, 6.5–7 × 4 mm, pink, elliptic-obovate, apically obtuse, entire. Stamens 6, isomorphic and free; filaments complanate and glabrous, 3 mm long, declinate but incurved distally bringing the anthers to an incurved position opposing the style; anthers 2 mm long, 1 mm wide, pale yellow, turning brownish orange with age, oblong with two ventrally inclined pores at the broadly rounded apex; connective slightly thickened and dilated dorsally at the filament insertion into a short blunt spur up to 0.25 mm long. Ovary completely inferior, 2-celled, sparingly beset with stellate-lepidote hairs, glabrous at the summit surrounding the styler scar but not distended into a prominent cone or collar. Style declinate, incurved distally, glabrous, 5.5 mm long; stigma punctiform. Berry globose, 5–6 mm long and 4–7.5 mm in diameter. Seeds bluntly deltoid, 1–1.5 mm long, beige with a smooth glossy testa and conspicuous lateral raphe.

**PHENOLOGY.**—The only known flowering specimens were collected in February; fruiting collections have been made in February, September, October, and December.

**DISTRIBUTION.**—Endemic to the low cloud forests on Cerro Jefe in central Panama at 900–1,000 m (Fig. 8).

**ADDITIONAL SPECIMENS EXAMINED.**—PANAMA. Panamá: summit and S facing slopes of Cerro Jefe, 9 Feb. 1978, *Almeda & Nakai 3459* (CAS); Cerro Jefe, along trail on ridge running NE from summit, 18 Dec. 1974, *Mori & Kallunki 3755* (MO); Cerro Jefe, 29 Oct. 1980, *Sytisma 2007* (MO); Cerro Jefe, road leading N from summit, 26 Sep. 1975, *J. T. & F. Witherspoon 8552* (MO).

Collections of *T. hexandra* are few despite the fact that it is one of the most common shrubby epiphytes in the forest at the summit of Cerro Jefe. In the field, fertile material is evidently overlooked without the aid of binoculars, because the small flowers are produced on uppermost branchlets positioned high on host trees where access to sunlight is optimal.

*Topobea hexandra*, together with *T. cordata*, *T. caliginosa* and *T. crassifolia*, form a closely related species group best interpreted as a spe-

cialized evolutionary line within the genus. They are distinguished from other congeners by a combination of specialized features associated with great reduction in flower size. These are: (1) flowers sessile or short-pedicellate (2–3 mm) at anthesis; (2) diminutive petals (4.5–9 × 1.5–6 mm); (3) each flower has only six stamens, each of which is attached to the torus opposite a calyx lobe; and (4) the ovary is 2-celled or 4-celled. The stamen number in *T. crassifolia* and *T. caliginosa* was unknown to me when I described these taxa, because all available study material had flowers with detached stamens (Almeda 1980). Recent collections of these two species and *T. cordata* clearly show that they are all hexandrous. The reduction in stamen number exhibited by this group of species is otherwise unknown in the tribe.

Among its close allies, *T. hexandra* is most similar to *T. caliginosa*. Both species have 3-nerved leaves, translucent petals that have a liberal scattering of hyaline disc-shaped gland-like processes, and 2-celled ovaries. *Topobea caliginosa* differs in having glabrous uppermost nodes, oblanceolate to spatulate, basally attenuate leaf blades, confluent anther pores, and unappended anther connectives.

Within its restricted range, *T. hexandra* shows inconstancy in characters of the indument. Distal branchlets can either be glabrous or sparsely beset with spreading glandular hairs. When present these hairs are found on distal internodes, petioles of juvenile foliage, and on upper and lower surfaces of some young leaves, but most of the hairs appear to fall away with age. All specimens of the type collection are devoid of glandular hairs. *Mori & Kallunki 3755* and *Witherspoon 8552* are beset with hairs as described above, but *Almeda & Nakai 3459*, which consists of two branches, has hairs on one branch but not on the other. Unfortunately, *T. hexandra* is known from too few collections to determine which, if any, of these forms constitutes the prevalent condition.

The epithet for this species is derived from the Greek words *hex*, six, and *andros*, male, in reference to the 6-stamened flowers.

***Topobea parvifolia* (Gleason) Almeda, comb. nov.**

*Blakea parvifolia* Gleason, *Phytologia* 3:357. 1950.

**TYPE.**—PANAMA. Coclé: crest of Cerro Pajita, El Valle de Antón, 1,100 m, *Allen 3761* (holotype: NY; isotype: MO!).



In the protologue, Gleason described the anthers of *Blakea parvifolia* as acute and emarginate at the tip with each anther sac opening by a separate dorso-terminal pore (Fig. 3B). Because anthers of this kind can only be interpreted as those of *Topobea*, Gleason appears to have erred in placing this species in *Blakea* and subsequently maintaining it in that genus for his treatment of the family in the Flora of Panama (Gleason 1958). Gleason's brief discussion in the protologue also stated that "the one flower remaining had lost part of its petals and stamens but there was no evidence that there had been more than four of the one and eight of the other." My study of this species in the field and herbarium shows that it has stamens that are coherent in a ring, as noted by Gleason, but the flowers are consistently 6-merous with 12 stamens.

Despite the heightened collecting activity in Panama during the past decade, *T. parvifolia* is still known only from the windswept slopes and ridges in the vicinity of El Valle de Antón.

***Topobea suaveolens* Almeda, sp. nov.**

(Fig. 12)

TYPE: PANAMA. Veraguas: along trail to summit of Cerro Tute about ½ mile above the Escuela de Agricultura Alto Piedra near Santa Fe, elev. 900–1,100 m, 29 Jan. 1989, *Almeda et al.* 6484 (holotype: CAS; isotypes: AAU!, BM!, BRI!, CR!, DUKE!, FI, MEXU!, MICH!, MO!, NY!, PMA!, TEX!, US!).

Arbor epiphytica 4 m. Ramuli primum sulcato-quadrangulati demum teretes glabri; linea interpetiolaris paulo elevata evoluta. Petioli 1.1–1.8 cm longi; lamina 3.6–5.3 × 1.6–2.5 cm elliptica apice acuminata vel caudato-acuminata basi acuta, 3-plinervata, nervi in axillis acaromatitiis instructi, subcoriacea et integra, nervis secundariis 0.25 mm inter se distantibus. Flores 6-meri penduli in quoque nodo superiore singuli, pedicellis, 2.3–3 cm longis; bractea omnino liberae; bractea exteriores 4.5–7.5 × 3–4 mm ellipticae vel ovato-ellipticae apice acuto vel rotundato; bractea interiores 4–4.5 × 4 mm ovatae vel suborbiculares apice rotundato. Hypanthium (ad torum) 4 mm longum extus glabrum; calycis tubus 1.5 mm longus, lobis 1 mm longis. Petala 1.2–1.5 × 0.9–1.1 cm obovata apice rotundato. Filamenta 2.5–3.5 mm longa; antherae 2.5 × 1 mm oblongae inter se lateraliter non cohaerentes, poro unico dorsaliter inclinato; connectivum nec prolongatum nec appendiculatum. Stylus 8.5–9 mm; ovarium 6-loculare et ½ inferum apice glabro (cono et collo non evoluto).

Epiphytic trees to 4 m tall, often obscuring and overtaking the crowns of host trees. Distal branchlets quadrate to quadrisulcate and glabrous with well-defined interpetiolar ridges or lines. Vegetative buds deciduously lepidote-furfuraceous. Mature leaves of a pair equal or slightly unequal in size, glabrous throughout; petioles 1.1–1.8 cm long; blades subcoriaceous, 3.6–5.3

cm long and 1.6–2.5 cm wide, elliptic, apex acuminate to caudate-acuminate, base acute, margin entire, 3-plinerved with an additional inconspicuous pair of submarginal veins and numerous striolate transverse secondary veins spaced mostly 0.25 mm apart at the widest portion of the blade, pocket domatia typically formed abaxially in the angle between the median vein and the two proximal lateral veins. Flowers pendant and solitary in the leaf axils of uppermost branches; pedicels 2.3–3 cm long, glabrous. Floral bracts sessile, glabrous, entire, and free to the base; outer bracts 4.5–7.5 × 3–4 mm, elliptic to elliptic-ovate, apex bluntly acute to rounded; inner bracts 4–4.5 × 4 mm, ovate to suborbicular, apex broadly rounded. Hypanthia (at anthesis) campanulate, 4 mm long to the torus and 5.5–6 mm in diameter, glabrous. Calyx tube 1.5 mm long; calyx lobes 1 mm long and 4 mm wide basally, broadly ovate to deltoid-ovate with a blunt callose-thickened tooth on the abaxial apex of each lobe, margin entire, glabrous on both surfaces. Petals 6, glabrous, connivent to somewhat imbricate and bell-like when fully expanded, 1.2–1.5 × 0.9–1.1 cm, white flushed with dark pink along a broad continuous margin, obovate, apically rounded, entire. Stamens 12, isomorphic, free and encircling the exerted style; filaments complanate and glabrous, 2.5–3.5 mm long; anthers 2.5 mm long, 1 mm wide, yellow, laterally compressed, oblong in ventral view and narrowly ovoid in profile view with a shallow dorso-basal depression at the filament insertion, tipped with a solitary, dorsally inclined pore 0.75 mm in diameter; connective simple. Ovary ½ inferior, 6-celled, dilated at the glabrous summit into a smooth gentle dome 1–1.5 mm high. Style straight, glabrous, 8.5–9 mm long; stigma truncate. Berry globose, 5–6 mm long and 6–7 mm in diameter. Seeds narrowly and irregularly pyriform, 0.75–1 mm long, pale brown with a smooth testa and prominent lateral raphe.

PHENOLOGY. — The three known collections of this species which are in flower and fruit were collected in January, February, and March.

DISTRIBUTION. — Known only from the cloud forests of Cerro Tute in west-central Panama at 850–1,100 m (Fig. 8).

ADDITIONAL SPECIMENS EXAMINED. — PANAMA. Veraguas: vicinity of Cerro Tute, along trail to summit, 08°30'N, 81°07'W, 19 Mar. 1987, *McPherson 10654* (CAS); near Cerro Tute-Arizona, above Santa Fe and Alto de Piedra, 8°30'N, 81°10'W, 5 Feb. 1988, *McPherson 12043* (CAS).

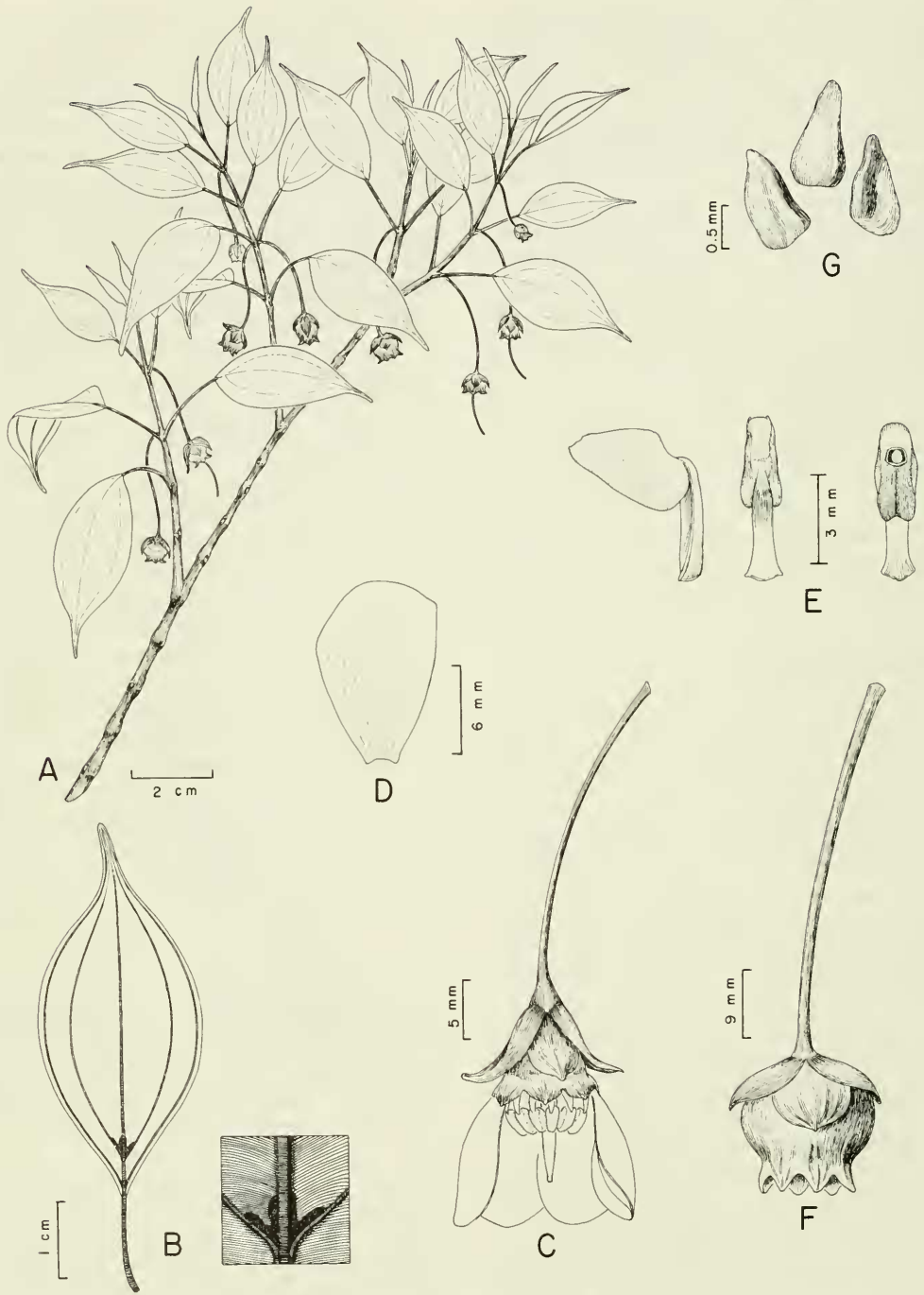


FIGURE 12. *Topobea suaveolens* Almeda. A, habit; B, representative leaf (abaxial surface) with enlargement showing domatium; C, flower (natural posture); D, petal (adaxial surface); E, stamens, lateral view (left), dorsal view (middle), ventral view (right); F, berry with persistent decussate bracts; G, seeds. (A-F from the holotype; G from *McPherson 10654*.)

*Topobea suaveolens* is unusual in having flowers that are bell-like and pendant with free connivent anthers that form a ring around the exerted straight style. This floral syndrome is not found in the other species of *Topobea* with brightly colored petals. *Topobea suaveolens* is clearly a sister species of *T. fragrantissima* (also described above). In addition to differences noted in the discussion of the latter, *T. suaveolens* is distinctive in at least two other floral features. Its filaments are conspicuously broadened at the base (Fig. 12E), and its shorter, laterally compressed anthers are narrowly ovate in profile view and have a conspicuous dorso-basal depression.

The strong vegetative similarities between *T. suaveolens* and *T. fragrantissima* can make identification of fruiting specimens difficult. Although *T. suaveolens* is known from few collections, even sterile material can be distinguished by the peculiar foliar pocket domatia that are formed abaxially in the angle between the midvein and the two proximal lateral veins (Fig. 12B).

Perhaps the most remarkable feature of this species is its agreeable floral fragrance. I described it as fruity (*Almeda 6484*), but a more telling comparison likens it to grape-flavored chewing gum (*McPherson 12043*). The name for this species is derived from *suavis*, Latin for sweet, in reference to the sweet-smelling flowers.

#### ACKNOWLEDGMENTS

This study was supported, in large part, by U.S. National Science Foundation Grant BSR 8614880 (Flora Mesoamericana) and the G. Lindsay Field Research Fund of the California Academy of Sciences. For field assistance and/or special technical support in the herbarium I thank Bruce Bartholomew, Thomas F. Daniel, Greg de Nevers, Gordon McPherson, Kei Nakai, Orbelia R. Robinson, and Colleen Sudekum. For logistical support in the field, special thanks go to the Museo Nacional de Costa Rica, the Missouri Botanical Garden, the Organization for Tropical Studies, and the Smithsonian Tropical Research Institute. I am also grateful to John J. Wurdack for a review of the manuscript; Varsha C. Patel for information on pollen morphology; Ellen del Valle for the line drawings; Gina Umaña Dodero for reviewing the Spanish summary; and the curators and staffs of the following herbaria (acronyms fide Holmgren et al. 1981) for loans, gifts, or special assistance during study visits:

BM, BR, CM, CR, DUKE, F, K, MEXU, MO, NY, P, PMA, TEX, US, WIS.

#### RESUMEN

*Blakea* y *Topobea*, los únicos géneros en la tribu Blakeeae, están íntimamente relacionados, pero las anteras de *Topobea* tienen tecas lineal-oblongas, con uno o dos poros dorso-apicales o dos poros ventro-apicales. *Topobea* es un género con más de 60 especies descritas, incluido en *Blakea* solamente por Don, Baillon y Macbride, pero es muy útil reconocerlo hasta que dispongamos de una monografía. Se presenta una historia taxonómica de los dos géneros con un comentario sobre las características de las anteras empleado originalmente por Browne, Aublet, Cogniaux, y otros botánicos. Las diferencias genéricas a menudo se han alterado un poco para reflejar mejor las características inusuales de algunas especies que se encuentran en las montañas de Costa Rica y Panamá. Se provee una clave nueva para los dos géneros. Se describen cuatro especies nuevas de *Blakea* (*B. gregii*, *B. hammelii*, y *B. herrerae* de Panamá; y *B. scarlatina* de Costa Rica y Nicaragua), y tres especies nuevas de *Topobea* (*T. fragrantissima*, *T. hexandra*, y *T. suaveolens* de Panamá) y se transfieren tres especies de *Blakea* a *Topobea*. Estos cambios se basan en características de las anteras. Se proveen descripciones, ilustraciones y discusiones sobre las afinidades entre las especies nuevas. Además se presentan notas sobre polinización y mapas de distribución.

#### LITERATURE CITED

- ACKERMAN, J. D. 1986. Coping with the epiphytic existence: pollination strategies. *Selbyana* 9:52-60.
- ALMEDA, F. 1980. Central American novelties in the genus *Blakea* (Melastomataceae). *Rhodora* 82:609-615.
- . 1981a. *Blakea penduliflora* (Melastomataceae): a new green-flowered species from Costa Rica. *Brittonia* 32(4):508-511.
- . 1981b. New and reconsidered species of *Miconia* (Melastomataceae) from Costa Rica and Panama. *Proc. Calif. Acad. Sci.* 42(10):303-314.
- . 1989. Five new berry-fruited species of tropical American Melastomataceae. *Proc. Calif. Acad. Sci.* 46(5): 137-150.
- . In press. Melastomataceae. In *Flora de Nicaragua*. W. D. Stevens, ed. Missouri Botanical Garden, St. Louis.
- AUBLET, J. B. C. F. 1775. *Histoire des plantes de la Guiane française*. London and Paris. 4 vols. (*Topobea*, 1:476, t. 189.)
- BAILLON, H. E. 1879. Mélastomacées. *Hist. Pl.* 7:1-65. (English transl. 7:1-65. 1881.)
- BENTHAM, G. AND J. D. HOOKER. 1867. Melastomaceae. *Genera plantarum* 1(2):725-773.

- BROWNE, P. 1756. The civil and natural history of Jamaica in three parts. London. (*Blakea*, p. 323, t. 34.)
- BUCHMANN, S. L. 1983. Buzz pollination in angiosperms. Pp. 73–113 in *Handbook of experimental pollination biology*. C. E. Jones and R. J. Little, eds. Van Nostrand Reinhold Co., Inc., New York, New York.
- CANDOLLE, A. P. DE 1828. Melastomaceae. In *Prodromus systematis naturalis regni vegetabilis* 3:99–202.
- COGNIAUX, A. 1888. Melastomaceae (*Blakea*). In C. F. P. von Martius, *Flora Brasiliensis* 14(4):558–564.
- . 1891. Mélastomacées. In A. and C. de Candolle, eds. *Monographiae phanerogamarum* 7:1–1256. G. Masson, Paris.
- DON, D. 1823. An illustration of the natural family called Melastomataceae. *Mem. Wern. Nat. Hist. Soc.* 4:276–329.
- GLEASON, H. A. 1935. Melastomaceae. In A. Pulle, ed. *Flora of Surinam* 3:178–281. J. H. de Bussy Ltd., Amsterdam.
- . 1945. On *Blakea* and *Topobea*. *Bull. Torrey Bot. Club* 72(4):385–393.
- . 1947. Additional notes on *Blakea* and *Topobea*. *Phytologia* 2:279–281.
- . 1950. Observations on tropical American melastomes. *Phytologia* 3:345–360.
- . 1958. Melastomataceae. In R. E. Woodson, Jr. and R. W. Schery, eds. *Flora of Panama*. Ann. Missouri Bot. Gard. 45:203–304.
- HOLMGREN, P. K., W. KEUKEN, AND E. K. SCHOFIELD. 1981. *Index Herbariorum*. Part I, 7th ed. The herbaria of the world. *Regnum Veg.* 106:1–452.
- HOWARD, R. 1983. The plates of Aublet's *Histoire des plantes de la Guiane française*. *J. Arnold Arbor.* 64:225–292.
- JACOBS, M. 1966. On domatia—the viewpoints and some facts. I, II, III. *Proc. Koninkl. Nederl. Akad. Wetensch.* C69: 275–316.
- JUSSIEU, A. L. DE. 1789. *Genera plantarum*. Paris.
- KOEK-NOORMAN, J., P. HOGEWEG, W. H. M. VAN MAANEN, AND B. J. H. TER WELLE. 1979. Wood anatomy of the *Blakeaceae* (Melastomataceae). *Acta Bot. Neerl.* 28:21–43.
- LINNAEUS, C. 1759. *Systema naturae*. Vol. 2, 10th ed. Stockholm. (Facsimile ed. by J. Cramer, Weinheim, 1964.)
- LINNAEUS, C., VON FILIUS 1781. *Supplementarum plantarum*. Braunschweig.
- LUMER, C. 1981. Rodent pollination of *Blakea* (Melastomataceae) in a Costa Rican cloud forest. *Brittonia* 32(4): 512–517.
- LUMER, C. AND R. D. SCHOER. 1986. Pollination of *Blakea austini-smithii* and *B. penduliflora* (Melastomataceae) by small rodents in Costa Rica. *Biotropica* 18(4):363–364.
- LUNDSTRÖM, A. N. 1887. Pflanzenbiologische studien II. Die anpassungen der pflanzen an thiere. I. Von domatia. *Nova Acta Regiae Soc. Sci. Upsal.* (Ser. 3) 13(10):1–88.
- MACBRIDE, J. F. 1941. Melastomataceae. In *Flora of Peru*. *Field Mus. Nat. Hist., Bot. Ser.* 13:249–521.
- NAUDIN, C. 1852. Melastomacearum monographicae descriptionis. *Ann. Sci. Nat.* III, 18:85–154.
- PATEL, V. C., J. J. SKVARLA, AND P. H. RAVEN 1985. Pollen characters in relation to the delimitation of Myrtales. *Ann. Missouri Bot. Gard.* 71:858–969.
- PEMBERTON, R. W. AND C. E. TURNER 1989. Occurrence of predatory and fungivorous mites in leaf domatia. *Amer. J. Bot.* 76(1):105–112.
- RENNER, S. S. 1989. A survey of reproductive biology in neotropical Melastomataceae and Memecylaceae. *Ann. Missouri Bot. Gard.* 76:496–518.
- ROUBIK, D. W. 1989. *Ecology and natural history of tropical bees*. Cambridge University Press, Cambridge, England.
- SOLT, M. L. AND J. J. WURDACK 1980. Chromosome numbers in the Melastomataceae. *Phytologia* 47:199–220.
- SPACE, C. A. 1965. Cuticular studies as an aid to plant taxonomy. *Bull. Brit. Mus. (Nat. Hist.), Bot.* 4(1):1–78.
- STANDLEY, P. C. 1924. Melastomaceae. In *Trees and shrubs of Mexico*. *Contr. U.S. Natl. Herb.* 23(4):1046–1074.
- . 1938. Melastomaceae. In *Flora of Costa Rica*. *Field Mus. Nat. Hist., Bot. Ser.* 18(3):783–845.
- STANDLEY, P. C. AND L. O. WILLIAMS. 1963. Melastomaceae. In *Flora of Guatemala*. *Fieldiana, Bot.* 24:407–525.
- STEIN, B. A. AND H. TOBE. 1989. Floral nectaries in Melastomataceae and their systematic and evolutionary implications. *Ann. Missouri Bot. Gard.* 76:519–531.
- TRIANA, J. 1871. Les Mélastomacées. *Trans. Linn. Soc. London* 28:1–188.
- WELLE, B. J. H. TER AND J. KOEK-NOORMAN. 1981. Wood anatomy of the neotropical Melastomataceae. *Blumea* 27: 335–394.
- WILLIAMS, N. H. 1983. Floral fragrances as cues in animal behavior. Pp. 50–72 in *Handbook of experimental pollination biology*. C. E. Jones and R. J. Little, eds. Van Nostrand Reinhold Co., Inc., New York, New York.
- WURDACK, J. J. 1973. Melastomataceae. In T. Lasser, ed. *Flora de Venezuela* 8:1–819.
- . 1980. Melastomataceae. In G. Harling and B. Sparre, eds. *Flora of Ecuador* 13:1–406.